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Stream Capture and the Distribution of the Percid Fish *Etheostoma sagitta*, with Geologic and Taxonomic Considerations[1]

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ROBERT A. KUEHNE AND REEVE M. BAILEY

THE arrow darter, *Etheostoma sagitta* (Jordan and Swain), long poorly known, was redescribed by Bailey (1948). This endemic of the upper Cumberland River system was shown to be allied to *Etheostoma nianguae* Gilbert and Meek from the lower Missouri River system and to *Etheostoma spilotum* Gilbert from the upper Kentucky River system. The subgenus *Litocara* was erected for this small group, which was assigned to the genus *Poecilichthys*. Subsequently (Bailey and Gosline, 1955; Bailey, Winn, and Smith, 1954), *Poecilichthys* was incorporated with *Etheostoma*, and *Litocara* submerged into the subgenus *Oligocephalus*, in which *E. sagitta* and its relatives may best be ranked merely as a species group. The intimate relationship between *sagitta* and *spilotum* was noted by Bailey (1948) who suggested that *spilotum* was derived from *sagitta* by differentiation following its entrance into the Kentucky system by stream capture. Comparison was rendered difficult, however, by the lack of adequate material of *spilotum*; only two poorly preserved specimens were available for study.

We are now able to report the analysis of newly collected material of all three forms of the *sagitta* group, and the investigation of the topography of the watershed between the upper Kentucky and upper Cumberland drainages. In brief, our study discloses close agreement in most characters between *sagitta* and *spilotum*, with differentiation in scale size and development of the lateral line. *E. spilotum* is treated as a subspecies of *sagitta*. The upper part of Collins Fork, now in the Kentucky River drainage, is interpreted as having been transferred by headwater piracy from its former connection with Little Richland Creek of the Cumberland drainage. This change is believed responsible for the entry of *Etheostoma sagitta* into the Kentucky River system, where subspecific differentiation has occurred.

[1] This study was facilitated by a grant from the Horace H. Rackham School of Graduate Studies of The University of Michigan.

THE *Etheostoma sagitta* SPECIES GROUP

Etheostoma nianguae Gilbert and Meek.—Through the kindness of Drs. Frank Cross and Arthur Witt, Jr. we have examined specimens of *nianguae* in the collections of the University of Kansas (KU) and University of Missouri (UMoMZ), respectively. The records listed below, all from the Osage River system in Missouri, include all known specimens of the species except for the original types from the Niangua River near Marshfield, Webster County, Missouri (Gilbert and Meek in Gilbert, 1887:52). Missouri Conservation Department, 2 specimens, 74 and 77 mm., Niangua River, 5 mi. southeast Buffalo, T. 33 N., R. 19 W., sec. 22, Dallas Co. UMMZ (University of Michigan Museum of Zoology) 150472, 92 mm., Barren Fork of Tavern Cr., 5 mi. northwest Iberia, T. 39 N., R. 13 W., sec. 10, Miller Co. UMoMZ 1884, 102 mm., Barren Fork of Tavern Cr., 5 mi. northwest Iberia, T. 39 N., R. 13 W., sec. 3, Miller Co. UMMZ 152703 (3), 55-72 mm., Barren Fork of Tavern Cr., 7 mi. southeast Tuscumbia, Miller Co. UMMZ 152799, 77 mm., Tavern Cr., 2 mi. northeast Iberia, Miller Co. UMoMZ 1883, 86 mm., Big Tavern Cr., 6 mi. north Iberia, T. 40 N., R. 13 W., sec. 25, Miller Co. UMoMZ 1885, 54 mm., and KU 5131 (6), 42–69 mm., Little Maries R., 1 mi. southwest Westphalia, T. 43 N., R. 10 W., sec. 34, Osage Co. UMoMZ 1881 (1) and 1882 (2), 45–51 mm., Maries R., 0.5 mi. south Westphalia, T. 43 N., R. 10 W., sec. 35, Osage Co.

The range of *Etheostoma nianguae* (Fig. 1) as indicated by the above records is restricted to clear southern tributaries of the lower Osage River in southcentral Missouri. Bailey (1948) included the Gasconade River in the stated range of the species. This was a *lapsus* or was based on hearsay evidence which cannot now be confirmed. Dr. Witt and Mr. Perry Robinson, who are familiar with the ecology of the species and the area involved, doubt that the species occurs in the Gasconade River drainage. *E. nianguae* is known to inhabit

clear, gravel-bottomed creeks of small to medium size. Whether the species enters very small intermittent brooks such as those seemingly preferred by *E. sagitta spilotum* is not known.

Etheostoma nianguae is a well-defined species. It shares most characters (Tables 1 and 3) and is superficially similar to *E. sagitta*, but from that species it differs as indicated in the accompanying key and in Tables 2 and 3. *E. nianguae* may also attain a somewhat larger size. The largest individual seen is 102 mm. in standard length; the largest of *E. s. sagitta* is 81 mm. and of *E. sagitta spilotum* is 84 mm. The marked gap in range between *nianguae* and the other forms of the *sagitta* species group is consistent with its structural distinctiveness.

Etheostoma sagitta sagitta (Jordan and Swain).—In addition to the records given by Bailey (1948) for the upper Cumberland River system in Kentucky we may now add: UMMZ 165456, 37 mm., Puckett Creek, 4 mi. southwest Wallins, Bell Co. UMMZ 168078, 45 mm., Clear Fork, Cumberland River, highway 471, 2 mi. northeast Jellico, Whitley Co. UMMZ 171533 (2), 34 and 73 mm., Wolf Creek, 3.1 mi. west Pleasant View, highway 628, Whitley Co.

This subspecies is restricted to the Cumberland River system above Cumberland Falls (Fig. 1). All known localities are in Kentucky, but it probably occurs in tributaries to the Clear Fork of the Cumberland in Tennessee.

TABLE 1. FREQUENCY DISTRIBUTIONS OF FIN RAY COUNTS IN *Etheostoma nianguae* AND THE SUBSPECIES OF *E. sagitta*

Form	Dorsal Spines					Dorsal Soft Rays				
	IX	X	XI	XII	Mean	12	13	14	15	Mean
nianguae		2	14	3	11.05		2	17		13.89
sagitta	2	20	4		10.08	1	6	17	2	13.77
spilotum	1	31	28		10.45	8	33	19		13.18

	Anal Spines			Anal Soft Rays				
	I	II	Mean	9	10	11	12	Mean
nianguae	1	18	1.95		1	7	11	11.53
sagitta		26	2.00	1	8	14	3	10.73
spilotum	2	66	1.97	1	41	25	1	10.38

	Total Pectoral Rays (Both Sides)					
	28	29	30	31	32	Mean
nianguae		1	13	2	3	30.37
sagitta	3	2	19	—	1	29.76
spilotum	34	14	20	1		28.83

TABLE 2. FREQUENCY DISTRIBUTIONS OF SCALE COUNTS IN *Etheostoma nianguae* AND THE SUBSPECIES OF *E. sagitta*

Form	Scales in Lateral Series																													
	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	Mean
nianguae																						1	—	1	3	2	2	6	2	1	1	78.05
sagitta				1	—	—	1	—	4	3	4	3	2	1	1	4	1	1														62.96
spilotum	2	3	9	9	13	10	10	9	3	1																						56.43

	Scales in Transverse Series									
	15	16	17	18	19	20	21	22	23	Mean
nianguae						3	1	12	3	21.79
sagitta	1	3	6	6	6					17.59
spilotum	11	22	23	8	4					16.59

	Scales around Caudal Peduncle										
	18	19	20	21	22	23	24	25	26	27	Mean
nianguae							2	6	8	3	25.63
sagitta			1	—	6	16	4				22.81
spilotum	1	5	6	18	22	12					21.42

TABLE 3. DEVELOPMENT OF LATERAL LINE IN *Etheostoma nianguae* AND THE SUBSPECIES OF *E. sagitta*.[1]

Form	Pored Scales in Lateral Series															
	34–36	37–39	40–42	43–45	46–48	49–51	52–54	55–57	58–60	61–63	64–66	67–69	70–72	73–75	76–78	79–81	Mean
nianguae													2	5	7	4	75.89
sagitta						1	4	4	6	2	4						58.38
spilotum	2	4	8	14	11	17	6										45.84

	Unpored Scales in Lateral Series												
	0–1	2–3	4–5	6–7	8–9	10–11	12–13	14–15	16–17	18–19	20–21	22–23	Mean
nianguae	7	8	1	2									2.22
sagitta	2	6	5	6	—	2							4.57
spilotum			5	8	17	9	10	4	5	1	2	1	10.69

[1] Counts are given as class frequencies, but means are based on the ungrouped data which are derived only from fish more than 40 mm. in standard length.

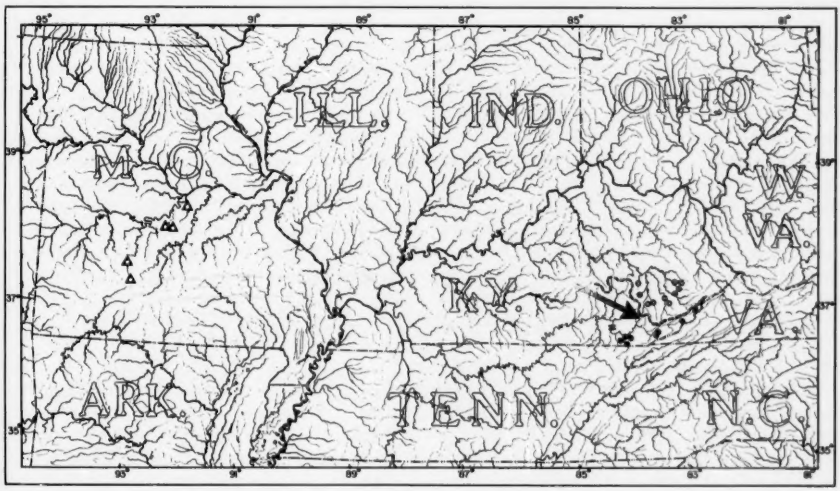

Fig. 1. Central United States showing the distribution by record stations of *Etheostoma nianguae* (triangles), *E. sagitta sagitta* (solid circles) and *E. sagitta spilotum* (open circles). The watershed between the Kentucky (to the north) and the Cumberland drainages is shown by a dashed line; the site of the stream capture across the watershed (Fig. 2) is indicated by an arrow. Cumberland Falls is denoted by a double bar.

Etheostoma sagitta spilotum Gilbert.—To the station records given by Gilbert (1887) and Woolman (1892) for the Kentucky River system in Kentucky we may now add: UMMZ 167983 (4), 35–36 mm., 6 mi. southeast Egypt, U. S. Highway 421, Clay Co. UMMZ 177325 (25), 38–69 mm., Clemons Fork of Buckhorn Cr. at entrance of John Carpenter Branch, 5 mi. east Noble, Breathitt Co. University of Kentucky, 64 mm., Troublesome Creek, 3 mi. east Dwarf, Knott Co. Univ. Ky. (72), 41–84 mm., Buckhorn Creek and tributaries (Clemons Fork, Laurel Fork, Bear Branch, Coles Fork, Lewis Fork, Millseat Branch, and Longs Fork), all within five miles of Noble, Breathitt and Knott counties.

THE STATUS OF *Etheostoma spilotum*

Etheostoma nianguae spilotum was described from Sturgeon Creek at Travelers

Rest, Owsley County, Kentucky. Seven additional localities, also located in the upper Kentucky River system, were recorded, as *E. spilotum*, by Woolman (1892:280, pl. 51, fig. 3). Since then no new collections have been reported.

In the spring of 1947, Norman J. Wilimovsky and Bailey revisited six of the eight known collection stations for *spilotum* in a vain effort to secure fresh material. A subsequent visit to the upper Kentucky basin in 1949 was similarly unsuccessful, but in 1954 a collection of four small specimens was obtained in the headwaters of Sextons Creek, Clay County. In 1959, while making a survey of the Buckhorn Creek basin and certain adjacent streams, Breathitt and Knott counties, Kuehne took the species at no less than 15 stations and obtained 98 specimens. The preferred habitat is small headwater creeks, often where such streams are reduced to intermittent pools. This darter, *Semotilus atromaculatus*, and *Campostoma anomalum*, are the most persistent upstream residents of these waters. At downstream stations, as more species are found and flow increases, *spilotum* becomes scarce or is absent.

Examination of the freshly caught specimens of *spilotum* and a comparison of them with Cumberland drainage specimens and with the color description of *sagitta* (Bailey, 1948) reveal close relationship between these forms. Indeed, preliminary study led us to suspect that they were identical. We find no consistent divergence in pigmentation, there are no observable differences in proportions, and fin-ray counts (Table 1) are in rather close agreement. Scale counts (Tables 2 and 3), however, indicate that *sagitta* has smaller scales and a better developed lateral line than does *spilotum*.

The most reliable character for separation of the two forms is the number of scales in the midlateral series (Table 2) with a line betwen 59 and 60 providing the most consistent distinction: 94.2 percent of Kentucky drainage specimens have fewer, 92.3 percent of Cumberland drainage specimens have more. Because small specimens may have an incomplete complement of pored scales, counts of pored and unpored scales are confined to fish over 40 mm. in standard length. Pored scales in the lateral series (Table 3) in *spilotum* number 34 to 54, with 52 or fewer in 93.5 percent of individuals; in *sagitta* there are 51 to 66, with 53 or more in 90.5 percent. The count of unpored scales in the lateral series is subject to considerable overlap. In *spilotum* there are 4 to 23, with 8 or more in 79.0 percent; in *sagitta* there are 0 to 10, with 7 or fewer in 90.5 percent. Scales in a transverse series (counted on a diagonal from the first dorsal soft ray downward and backward to the anal base or the midventral line) differ but little between *spilotum* and *sagitta* (Table 2), but these forms are readily separable from *nianguae* in this character. There is wide overlap in caudal peduncle scale count, but 81.2 percent of individuals of *spilotum* have 22 or fewer and 74.0 percent of specimens of *sagitta* have 23 or more.

The forms *sagitta* and *spilotum* are allopatric so interbreeding in nature is impossible. They have differentiated to the extent that a high percentage of individuals can be correctly allocated structurally, but slight character intergradation exists. The ranges of the forms are close geographically and they are presumably subjected to closely similar environmental conditions. It is believed, therefore, that the observed differences have a genetic basis, an interpretation that receives support from consistency among the several samples from each drainage. (Pectoral count shows considerable difference among the samples of *spilotum* and may be subject to environmental modification, but this character is not involved in the separation of the forms.) In view of these data we believe that *sagitta* and *spilotum* are best treated as subspecies (Bailey, Winn, and Smith, 1954:148–50).

Key to Forms of the *Etheostoma sagitta* Species Group

1a.—Scales in lateral series on body 73 to 82; in transverse series 20 to 23. Pored lateral scales 71 to 81; unpored scales in lateral series 0 to 7, usually 0 to 3. Caudal peduncle scale rows 24 to 27. Cheek with a few scales behind and below eye. Typically with 2 discrete, jet-black, circular spots at base of caudal fin, these rarely conjoined. *Southern tributaries to the lower Osage River, southcentral Missouri* . . . . . Niangua darter, *Etheostoma nianguae*

1b.—Scales in lateral series 52 to 69; in transverse series 15 to 19. Pored lateral scales 34 to 66; unpored scales in lateral series 0 to 23, usually 4 or more. Caudal peduncle scale rows 18 to 24. Cheek scaleless. A single, dark, vertically elongate spot at base of caudal fin.

Arrow darter, *Etheostoma sagitta* 2

2a.—Scales in lateral series 55 to 69 (60 or more in 92 percent). Pored scales in lateral

series 51 to 66 (53 or more in 90 percent). Unpored scales 0 to 10 (7 or fewer in 90 percent). Caudal peduncle scales 20 to 24 (23 or 24 in 74 percent). *Cumberland River system above Cumberland Falls, Kentucky and, perhaps, Tennessee* ..... *Etheostoma sagitta sagitta*

2b.—Scales in lateral series 52 to 61 (59 or fewer in 94 percent). Pored scales in lateral series 34 to 54 (52 or fewer in 93 percent). Unpored scales 4 to 23 (8 or more in 79 percent). Caudal peduncle scales 18 to 23 (22 or fewer in 81 percent). *Upper Kentucky River System, Kentucky* ..... *Etheostoma sagitta spilotum*

Stream Capture

Most of the divide between the Cumberland and Kentucky rivers is marked by distinct ridges with headwater tributaries separated by elevations of one hundred to several hundred feet (U. S. Geological Survey, quadrangle maps, 1952 series). In the Fount and Heidrick quadrangles, however, several gaps and low saddles disrupt the typical pattern. A state highway and a railroad utilize two of the best developed gaps as lowland connections between the river basins.

Two fine examples of stream capture are evident in this area (Fig. 2). Paynes Creek, formerly the headwaters of Fighting Creek, is now tributary to Little Richland Creek. Both Paynes and Fighting creeks lie in a continuous, well-developed valley, yet the lower branches of Paynes Creek are barbed and have reversed flow. After leaving its old valley the creek is abruptly diverted to the north-northwest through a narrow gorge, from which it emerges into the valley of Little Richland Creek. Since both Fighting and Little Richland creeks lie in the Cumberland River drainage, this stream piracy is of no apparent significance to the dispersal of fishes.

The stream capture involving the headwaters of Collins Fork, a present Kentucky River tributary, is perhaps less striking geologically, but is of notable importance biologically. The upper part of this creek lies in a well-developed valley that runs southeastward to join that of Little Richland Creek. Collins Fork now flows through this valley for about half its length, then turns eastward and northward and descends through a narrower valley of steeper gradient to join other Kentucky River tributaries. The southernmost branch of upper Collins Fork is barbed and flows "up" the valley to join the main creek at the point of diversion. The present divide between the Kentucky and Cumberland basins cuts across the dry valley floor about at its widest spot. The elevation here is little more than 10 feet above headwater tributaries of the two rivers, and it is here that Kentucky highway 11 crosses the divide. The above geomorphic evidence clearly indicates that upper Collins Fork was once tributary to Little Richland Creek but has been diverted into the Kentucky system by headwater capture.

Excepting the upper Collins Fork area, streams on the Kentucky River side of the divide have cut their valleys to depths at least 50 feet lower than streams on the Cumberland River side. In both elevation and gradient the upper part of Collins Fork is similar to Cumberland tributaries. The differential in elevation explains the direction of capture in this case, and the topography indicates that any future stream piracy in this region will likely divert Cumberland headwaters into the Kentucky system.

Rocks of the area are Pennsylvanian in age, belonging to the extensive Pottsville series. The Pottsville has been divided into recognizable units, even formations (McFarlan, 1943), but detailed lithological mapping is yet to be accomplished. McFarlan stated that sandstones and shales predominate, with hard sandstones normally capping the ridges. The areas of stream capture are composed of loose shales that are easily eroded in comparison to the sandstones that normally form the watershed divide.

The biologically important stream capture can be interpreted as resulting from a small Kentucky River tributary (lower Collins Fork in Fig. 2) eating through the resistant ridge material and then rapidly moving headward in loose shales to behead a Cumberland River tributary (upper Collins Fork in Fig. 2). The several low gaps in the region, all of which are in unconsolidated shales, indicate that the headwater erosion processes are still quite active. It would be difficult to date the stream capture accurately, though present indications are that it is a matter of a few thousand years at most. The notch cut at the point of capture is about 20 feet deep. The sediments at this point are completely unconsolidated and the gradient below the point of capture is fairly steep; thus the erosion may have been accomplished rather rapidly.

Erosion aided by a steep gradient is proceeding up a gap just east of the site of the

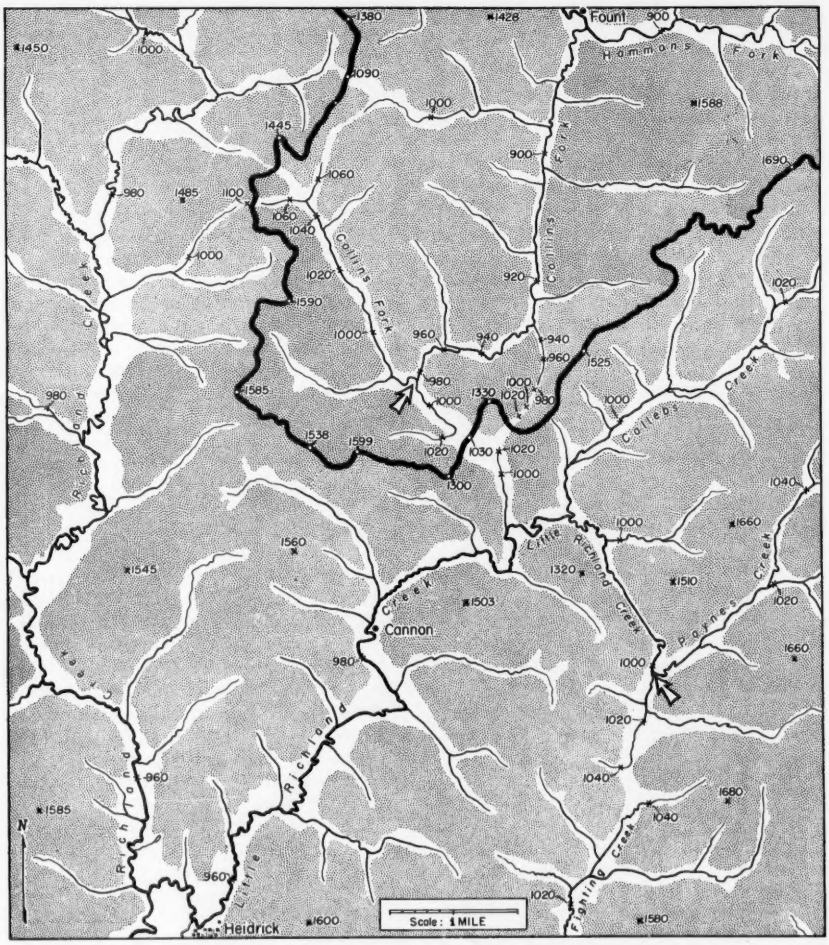

Fig. 2. Map showing drainage features along part of the watershed (heavy black line) of the Kentucky and Cumberland river basins, Knox County, Kentucky. Arrows indicate two points of stream capture. Shaded areas are uplands; selected ridge elevations in feet above mean sea level are given. Light areas approximate the width of the valleys and adjacent slopes to an elevation 40 feet above stream level. Valley elevations are indicated at points where 20 foot contour lines intercept streams. The upper part of Collins Fork, now in the Kentucky River system, formerly flowed southeast, then south into Little Richland Creek of the Cumberland basin. Paynes Creek, now tributary to Little Richland Creek, formerly flowed south into Fighting Creek. Other presumably older stream captures are suggested by valley configuration. Drafted from U. S. Geological Survey topographic sheets for Fount and Heidrick quadrangles.

Collins Fork piracy. A railway now traverses this gap. If geological processes are uninterrupted here it is likely that this eroding draw may eat headward and that Collins Fork will capture the upper part of Little Richland Creek.

The Stream Capture and Fish Dispersal

The upper part of Collins Fork, acquired by the Kentucky River system by stream capture, is a small creek which, when studied by Kuehne during a period of drought on September 27, 1959, was dry to intermittent

pools. Thus, it is to be expected that the only fishes available for transfer are those to be found in small hill streams of the upper Cumberland basin. Because of long isolation above the Cumberland Falls, that system is faunally depauperate. Most of the cyprinids and other fishes found here are widespread in the Ohio basin and are useless as faunal indicators.

Only four species of darters inhabit the upper Cumberland. Of these *Etheostoma kennicotti* is not known to occur in the Kentucky basin. It, like the cyprinid *Notropis galacturus,* was apparently not involved in stream transfer or was unsuccessful. *Etheostoma nigrum susanae,* an endemic subspecies of the upper Cumberland, is closely related to *Etheostoma nigrum nigrum,* which abounds in the Kentucky River system. The present stock in upper Collins Fork is typical *E. n. nigrum.* If *susanae* was transferred its gene pool has been absorbed or eliminated by the nominate subspecies. The two remaining darters, *Etheostoma sagitta* and the emerald darter, a species of *Etheostoma* of the subgenus *Ulocentra,* occur in the upper Cumberland and in the upper Kentucky basins. The emerald darter, but not the arrow darter, occurs also in the Rockcastle and South Fork of the Cumberland River below Cumberland Falls. Neither of these darters has close relatives anywhere in the central Ohio basin and we attribute their presence in the upper Kentucky to successful transfer by stream capture, probably by way of the Collins Fork piracy.

As indicated above, the Kentucky River stock of *E. sagitta* is readily distinguishable from that in the Cumberland basin. This may be due to differentiation following isolation. Alternatively, it is perhaps explainable on the basis of chance fixation of slightly atypical genes. It should be recalled that Collins Fork is a tiny stream, and if the transferred population was inbred from a nuclear stock with larger scales and a less well-developed lateral line than usual, the establishment of characters of the subspecies *spilotum* might be rapid. It may be hoped that geological research can date the stream capture. Study of the emerald darter is underway, but preliminary data indicate no important differences between stocks on opposite sides of the divide.

When sampled, upper Collins Fork was much modified not only by drought but by human utilization of the watershed. Regrettably, no specimens of *Etheostoma sagitta* or of *Etheostoma* (*Ulocentra*) sp. were obtained. Thirteen species of fishes were caught. Nine of these are forms that occur naturally or, like *Lepomis macrochirus,* through widespread introduction, on both sides of the divide.

Four forms, however, occur only on the Kentucky slope of the watershed: *Ericymba buccata, Etheostoma caeruleum, Etheostoma nigrum nigrum,* and *Etheostoma flabellare.* It is obvious that these species have invaded upper Collins Fork from lower Collins Fork since the stream capture. Had the stream capture moved *E. sagitta* from the Kentucky to the Cumberland drainage it would surely have transferred other common Kentucky basin forms simultaneously. Thus, the ichthyofaunal evidence as well as the geologic finding points to dispersal of the two darter species from the Cumberland to the Kentucky drainage.

Summary

The *Etheostoma sagitta* species group consists of two species and three forms; it is referred to the subgenus *Oligocephalus.* The distinguishing characters of the three forms are presented in tables of variation and in a key, and their distribution records are listed and mapped. *Etheostoma nianguae* is distinctive morphologically and is confined to the lower Osage River system in Missouri. *Etheostoma sagitta* consists of two subspecies, *E. s. sagitta,* an endemic form of the upper Cumberland basin, and *E. s. spilotum* of the upper Kentucky drainage. These subspecies overlap only slightly in scale counts, but appear to be indistinguishable otherwise.

Investigation of the topography of the watershed between the Cumberland and Kentucky rivers reveals a near-classical example of stream piracy between the drainages. Geologic and ichthyofaunal evidence indicates that piracy of upper Collins Fork as well as dispersal of the indicator fish species was from the Cumberland basin to the Kentucky system. The differentiation of *Etheostoma sagitta spilotum* from *E. sagitta sagitta* dates from the time of the stream capture, as yet unknown. In addition to *E. sagitta,* another darter, *E.* (*Ulocentra*) sp., gained access to the Kentucky River system as a result of the stream capture.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF KENTUCKY, LEXINGTON, KENTUCKY AND MUSEUM OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN.

Muscle Acetylcholinesterase Levels as an Index of General Activity in Fishes

MORRIS H. BASLOW AND ROSS F. NIGRELLI

THE work of Nachmansohn and his associates (1938, 1946) on the relationship between the enzyme acetylcholinesterase (ACHE), its physiological substrate, acetylcholine, and the voltage produced in the electric tissue of *Electrophorous electricus* (Linnaeus) demonstrated the direct relationship between the enzyme ACHE and neurological processes.

Since transmitted impulses are ultimately expressed as activity and motion, especially among lower forms, there should also be a quantitative relationship between observed physical activity and the level of this enzyme.

Using activity as a criterion, Marnay and his associate (1938, a,b,c) compared the enzymatic activity of the muscles of a tortoise, toad, frog and lizard, and from the data was able to correlate an increase in the enzyme with an increase in the general activity of these animals. Sawyer, (1943, 1944) working with *Amblystoma* and *Fundulus heteroclitus* (mummichog killifish) showed that the ability of the developing embryo to reach to mechanical stimulation at various stages was paralleled by an increase in cholinesterase activity.

The high levels of ACHE in fish reported by Augustinsson (1948) and the great differences in physical activity found among members of this group, suggested that an investigation of this apparent relationship would be of interest.

The assay used was an electrometric microtitration in which the optimal reaction pH of 8.0 is maintained by microliter aliquots of 0.01 N NaOH as indicated by a model G Beckman pH meter. Substrate autohydrolysis and dilution effects were measured and controlled. Tissue was homogenized in 0.85 percent saline, using a Waring Blendor and approximately 20 milligrams of tissue were used per assay added as a brei. The reaction volume was 25 milliliters and acetylcholine chloride at a concentration of 3×10^{-3M} was used as substrate. The reaction temperature was maintained at 26°C ± 0.5°C. Experimental conditions were such that acetylcholinesterase activity was measured. Lundin (1958, 1959) has shown that the cholinesterase of goldfish and guppy muscle is essentially acetylcholinesterase.

Muscle and brain tissue were removed, washed, blotted and weighed. Muscle was dissected free of nerve cord and other tissues in the smaller fishes. Posterior dorsolateral musculature was used in all cases. Brains were cut at the medulla-spinal cord junction and the optic stalks removed. Several species of invertebrates were analyzed as whole animals.

Enzymatic values are given as Nachmansohn's Q_{ACHE} = mgs. of ACH hydrolyzed by the enzyme contained in 100 mgs. of tissue per hour at 26°C.

To correlate the observed activity with enzymatic results, three impartial and competent ichthyologists (A, B and C) were

asked to grade each of the species used as: sluggish = 1; moderately active = 2; and active = 3. The three values were then averaged and used as semi-quantitative index of observed activity (Table 1).

Fish with index values in the range of 1–1.5 were placed in Group I (Sluggish), those with values from 1.5–2.5 were placed in Group II (Moderately active) and those with values from 2.5–3 were placed in Group III (Active). It can be seen in the following graph (Fig. 1) that a close relationship exists between the activity classification and the enzymatic levels of dorsolateral muscle.

Included in the first group are the sucker catfish (*Hypostomus plecostomus*) and the South American lungfish (*Lepidosiren paradoxa*). The sucker catfish has evolved the oral sucker, a mechanism which enables it to cope with rapidly flowing streams by attaching itself to some stationary object and waiting for food to pass by.

The elongate body, poor eyesight and small fins of the lungfish all suggest relative inactivity. It is often difficult to tell, using the criterion of slight motion, whether these fish are in a living or moribund state since they are almost always resting quiescently on the bottom of their enclosure. These remarkable fish are also capable of existing in a very inactive state for many years under conditions of dessication, when their swamp habitat periodically dries up.

In the moderately active group, most of the animals are modified so that they vary considerably from an efficient hydrodynamic form as described by Norman (1951). The mormyrid (*Gnathonemas petersi*) is strongly thigmotropic and feeds on bottom dwelling worms, which are ingested through an elongate, unique tubular mouth. This "browsing" habit does not suggest rapid motion and the fish usually lies quietly among plants and other objects in the tank.

The cichlidae, jack dempsey (*Cichlasoma biocellatum*) and mouthbreeders, (*Tilapia sp.*) represent a group of laterally compressed fishes which, like the mormyridae upon observation, are slow, methodical browsers unless frightened.

The swordtails (*Xiphophorus helleri*) and

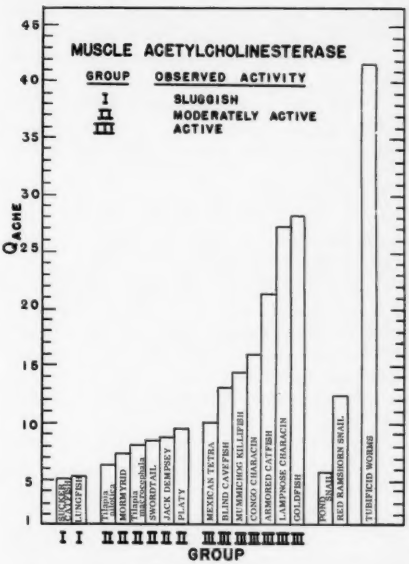

Fig. 1. Graphic relationship between activity classification of 15 species of fishes and three species of invertebrates and the enzymatic levels of dorsolateral muscle.

TABLE 1. RELATIONSHIP BETWEEN THE ENZYME ACHE AND THE ACTIVITY INDEX OF 15 SPECIES OF FISHES

Species[1]	Observers			Observed Activity Index Average	Number[1] of Animals	Mean Average QACHE	Average Deviation
	A	B	C				
Cichlasoma biocellatum	2	2	2	2.0	5	8.6	1.2
Distichodus sp.	2	2	2	2.0	1	16	
Barilius christyi	2–3	3	3	2.8	2	27.2	1.6
Hypostomus plecostomus	1	1–2	1	1.1	1	4.1	
Corydoras aeneus	1	2	3	2.0	1	21.3	
Tilapia macrocephala	2	2	2–3	2.1	4	8.0	2.5
Tilapia nilotica	2	2	2–3	2.1	2	6.3	
Lepidosiren paradoxa	1	1	1	1.0	1	5.4	
Gnathonemas petersi	2	1	2	1.6	3	7.3	3.4
Carassius auratus	2	2	2–3	2.1	6	28.2	3.3
Xiphophorus helleri	2	2	3	2.3	23	8.3	2.5
Xiphophorus maculatus	2	2	3	2.3	46	9.2	4.7
Fundulus heteroclitus	2	2–3	3	2.5	1	14.4	
Anoptichthys hubbsi	3	3	3	3.0	4	13.2	0.6
Astyanax mexicanus	3	3	2	2.6	4	10.1	1.0

[1] A number of these animals arrived at the laboratory as single specimens and the results of these assays are included as a matter of record.

platyfish (*Xiphophorus maculatus*) spend much of their time systematically examining the debris on the bottom of the aquaria in search of food.

A third group of fishes which may be classifield as "active" based on observations, have more streamlined bodies and are usually characterized by schooling behavior.

The armored catfish (*Corydoras aeneus*) lives on food material left behind by various predators. It is a voracious scavenger, constantly searching for food.

The tetras, Congo characin (*Distichodus sp.*), and lampnose characin (*Barilius christyi*) used for these studies approach the form of the bonito and other streamlined fishes and aggregate in schools which are in constant motion, as is the mummichog, (*Fundulus heteroclitus*).

The blind cavefish (*Anoptichthys hubbsi*) and their eyed river dwelling relatives, the Mexican tetra, (*Astyanax mexicanus*) are extremely nervous in temperament. These fish are even more favorable material for studies such as reported here because of the genetic differences which are manifested in the development of the eyes. Increased physical activity is associated with complete blindness. Rasquin (1949) states that: "The blind fish have no point of obstacle fixation and are constantly in motion. They consume more food than the river variety as their continual wandering evidentally calls for the expenditure of more energy."

There is a statistically significant difference between the mean values of the muscle acetylcholinesterase of the eyed river and blind cave forms. The observed increase in the physical activity of the blind fish is paralleled by a 30 percent increase in enzyme activity over the eyed form. Analysis of whole brain homogenates shows, however, that brain ACHE is significantly decreased in the blind form. The latter may be due to a loss of function in those associated areas of the brain dealing with sight and reactions to visual stimuli. Nachmansohn, Coates and Cox (1941) have shown that the various portions of the brain of the goldfish (*Carassius auratus*) differ in enzyme concentration with the greatest amount occurring in the optic lobes.

The brains of the Mexican tetra are larger than those of the blind cavefish (Table 2) but do not show the expected reduction in brain ACHE described by Weiss (1959).

In comparison, common tubificid worms whose habit is to move actively in order to aerate and feed themselves were analyzed as whole animals and compared to less active pond snails (*Physa gyrina*) and red ramshorn snails (*Planorbis sp.*). Again, in this case the worms were found to have a high Q_{ACHE} value (41.5) and the snails a low value (5.6 and 12.4 respectively). The unexpectedly high value found in the "tubifex" worms may be compared with the high acetylcholinesterase activity of a related nemertean worm cited by Kamamoto (1957).

TABLE 2. COMPARISON OF BRAIN AND MUSCLE ACHE BETWEEN *Astyanax mexicanus* AND *Anoptichthys hubbsi*

Species	Sex	Total Weight (Gm)	Brain Weight (Mg)	Muscle Q_{ACHE}	Brain Q_{ACHE}
Mexican tetra	F	4.8	19.5	9.6	41.6
Astyanax	F	3.4	11.0	12.1	62.5
mexicanus	M	3.6	21.5	8.8	48.0
	M	2.9	18.5	10.0	45.0
Average		3.6	17.6	10.1	49.2
Blind Cavefish	M	2.8	12.5	12.8	41.2
Anoptichthys	M	2.9	10.5	12.8	40.0
hubbsi	F	4.0	15.0	14.4	21.7
	F	5.6	19.5	12.6	23.3
Average		3.8	14.3	13.2	31.5

SUMMARY

Differences in the acetylcholinesterase levels of skeletal muscle in several species of fish have been found. These results have been correlated with the observed physical activity of these fishes, and their deviation from an efficient hydrofoil.

Mexican blind cavefish have higher muscle, and lower brain ACHE activity levels than the closely related Mexican tetra. These observations have been correlated with an increased physical activity and lack of vision in the cave fish.

Tubificid worms have been found to have a very high level of ACHE activity.

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NEW YORK AQUARIUM, CONEY ISLAND, BROOKLYN 24, NEW YORK.

Growth of an Antarctic Fish at Freezing Temperatures[1]

DONALD E. WOHLSCHLAG

INTRODUCTION

THE purpose of this study is to demonstrate the possibilities of age determination and the nature of growth of a common antarctic fish, *Trematomus bernacchii,* which lives almost continuously under ice cover in McMurdo Sound waters that remain near −1.9°C.

T. bernacchii is a benthic nototheniid fish which occurs around the Antarctic continent and some of the adjacent Antarctic islands (Norman, 1938). It is taken about eight times as frequently in baited traps or by hook and line as the several other bottom species at McMurdo Sound. The regular occurrence of this species in traps during the dark winter months (Mr. John Dearborn, personal communication) and the regular occurrence of benthos in the stomachs is evidence for considerable winter activity. A cursory examination of stomach contents indicates that any of the smaller bottom organisms might be utilized. Especially common in stomachs are such benthos as the polychaete "scale" worms, amphipods, and isopods; these invertebrates are generally quite abundant where fish occur. Remains of the large nemerteans and of bait discarded from traps and later found in the stomachs provide evidence that *T. bernacchii* is a scavenger as well as a carnivore.

Olsen's (1954, 1955) growth data for several South Georgian fishes, which live in somewhat warmer and much more open waters, are apparently the only comparative antarctic data; much more growth data are available for arctic species, many of which, however, live in waters as warm as 10°C or more in the brief summer. While Olsen's data indicate that the several South Georgian fishes grow more rapidly than many arctic species exposed to warmer summer seasons, it is not presently known whether a species living in much colder waters of uniform temperature can be aged on the basis of seasonal growth changes which are reflected in scale growth.

The relationship of the absolute growth rates of *T. bernacchii* to the metabolism of this species (Wohlschlag, 1960) should be especially interesting since the metabolic rates are relatively higher than arctic species (Scholander *et al.,* 1953; Wohlschlag, 1957) at the same given low temperatures. Comparisons of metabolic levels and growth rates of cold-adapted arctic and antarctic species with metabolic levels of species from warmer waters should eventually provide some insight into the efficiency of energy conversion of foods into growth, maintenance, and activity.

[1] Conducted under the U.S. Antarctic Research Program USARP); National Science Foundation Grant, NSF-G6338.

Age and growth data are also valuable in that age compositions of populations can be used to estimate mortality rates (Ricker, 1958, e.g.) and growth characteristics can be used to separate subpopulations (Cohen, 1954; Wohlschlag, 1954). Studies on growth and other adaptations of fish such as *T. bernacchii* found at an area almost permanently under sea ice cover should ultimately be of value in predicting and comparing such adaptations for any fish which may exist in the unexplored waters under the nearby permanently ice-covered Ross Ice Shelf.

This study was possible only with the efforts in planning and logistic support by the National Science Foundation's U. S. Antarctic Research Program Personnel and Navy Task Force 43. The aid of Messrs. John H. Dearborn and Hugh H. DeWitt was indispensable for work through the ice. Mrs. Galen Howard Hilgard supplied technical aid in preparing the fish scales for age and growth data and in making the statistical analyses.

Methods and Materials

Most *Trematomus bernacchii* used in this study were taken in the vicinity of the McMurdo Sound Naval Air Facility (77°51′S, 166°38′E), about 1 to 4 km. from the permanent ice cover of the Ross Ice Shelf. Small one-half inch mesh wire traps or hook-and-line fishing were utilized through cracks, seal holes, or blasted holes in the 2.5 to 3.0 meters of sea ice cover which persisted during the November 1958 to February 1959 period of sampling. At McMurdo Sound the areas fished were from Cape Armitage to Arrival Heights in depths of about 5 to 80 meters. Twenty-four specimens were also taken by hook-and-line from the U.S.S. Glacier anchored in waters about 16 meters deep at Terra Nova Bay (approximately 74°41.5′S, 164°37′E).

For each but two of 178 fish, weights, lengths, and scale samples were available; sex and gonad maturation data were available for all but the Terra Nova Bay specimens. All scale samples were from the broad flank just below the lateral line. Impressions of the sculpture on the scales were made in cellulose acetate plastic and the scales were "read" in the conventional manner at a magnification of 40 diameters. The total antero-lateral radius and the antero-lateral radii to the successive "annuli" were measured and recorded for each of 178 specimens.

Figure 1 illustrates the typical ctenoid nature of the *T. bernacchii* scales.

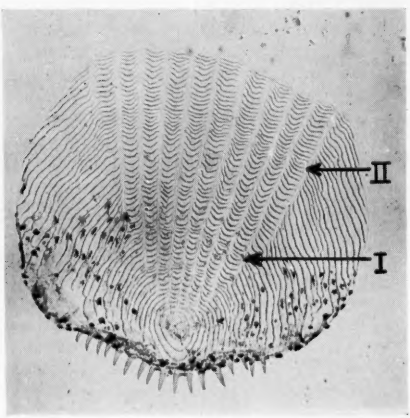

Fig. 1. Photograph of *Trematomus bernacchii* scale taken in August (midwinter) from immature specimen having a total length of 129 millimeters and weight of 27 grams. Cteni and focus are at posterior edge of scale. Note that breaks from "cutting over" of circuli at location of rings are especially prominent at posterior edge. Antero-lateral radius measurements (millimeters times 40) are: total, 74; to Ring I, 27; to Ring II, 56. Existence of a third ring between Ring II and the antero-lateral margin is questionable (see text).

Results

To determine whether scale length increases uniformly with body length and to establish a relationship which would suggest the size of fish at time of scale formation, the total lengths (mm.) of 176 fish were plotted against scale radii (mm. × 40) as shown in Fig. 2. Where L is the expected total length and S the magnified antero-lateral scale radius, the least squares linear equation for these 176 points is

$$L = 35.41 + 1.3901\ S.$$

Since males tend to be smaller than females, since there was a large proportion of the sample that was not sexed or immature, and since the plotted points of Fig. 2 possibly indicate a slightly sigmoid relationship, separate equations calculated for males, females, and fish (mostly immature) whose sex was not determined are respectively:

$$L = 43.84 + 1.3065\ S,$$
$$L = 43.20 + 1.3583\ S, \text{ and}$$
$$L = 34.27 + 1.3448\ S.$$

These equations suggest that the length of

Trematomus bernacchii at time of scale formation would be of the order of 40 mm.

An analysis of covariance of the regression of body lengths on scale lengths for males and females indicates (a) that mean body lengths "adjusted" for regression are not significantly different ($P \sim 0.10$) and (b) that the regressions 1.3065 and 1.3583 are also not significantly different ($P > 0.50$).

To establish the nature of regularity of growth rings, which could be interpreted as annuli on the scales, the average antero-lateral radii to successive rings and the total average radii for the nine age classes are tabulated (Table 1). Even with the relatively small numbers of specimens, there is a tendency for increase in radii with the increasing number of growth rings. The tendency is uniform enough to suggest that the rings are actually annuli.

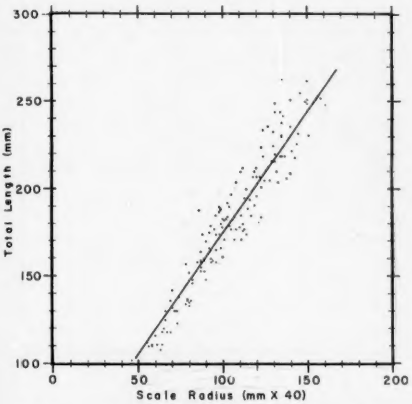

Fig. 2. Plot of total lengths (mm.) and antero-lateral scale radii (mm. × 40) for *Trematomus bernacchii* from McMurdo Sound.

Verification of the uniformity of body form for specimens of different sizes, sexes, and degrees of sexual maturity is possible by the use of simple weight-length relationships. The appropriate linear regressions of log weight (grams) on log total length (millimeters) are:

All fish: Expected log weight = −5.6519 + 3.3577 log length; N = 176.

Females: Expected log weight = −5.5004 + 3.2916 log length; N = 59.

Males: Expected log weight = −5.4497 + 3.2759 log length; N = 51.

Sex not known: Expected log weight = −5.7332 + 3.3894 log length; N = 66.

The equation for all fish plotted in exponential form with the data for individual fish is in Fig. 3. While the data show a uniform relationship between weight and length with relatively little dispersion, they also indicate definitely that the females grow much larger than males. The above equations, however, demonstrate the similarity between the body form of the two sexes in so far as body mass reflects body form.

For the above equations only those fish definitely known to be males or females are in the respective sex categories, while the immature fish and the few larger fish whose sex was not determined are in the "sex not known" class. For this reason, the smaller, immature fish alone would probably

TABLE 1. AVERAGES OF ANTERO-LATERAL SCALE RADII TO SUCCESSIVE RINGS AND TO SCALE EDGES IN *Trematomus bernachii* FROM MCMURDO SOUND[1]

Number of Fish			Number of Rings									Average Antero-lateral Radius
Males	Females	Total[2]	1	2	3	4	5	6	7	8	9	
1	—	6	24.7									55.7
—	—	12	28.5	53.8								67.8
15	3	34	24.9	45.2	68.1							87.0
19	5	32	25.4	44.8	66.0	87.3						100.8
14	16	44	27.6	43.1	64.8	86.1	104.1					120.5
2	20	31	24.9	42.1	62.5	82.2	102.6	122.5				132.9
—	9	13	23.6	40.3	59.2	80.6	96.9	114.9	128.2			137.8
—	4	4	19.5	36.0	54.5	75.5	93.5	110.0	129.3	137.3		148.0
—	2	2	24.5	39.0	50.0	65.5	78.0	87.5	103.5	121.5	134.5	162.0
51	59	178										

[1] Radii in millimeters times 40 diameters.
[2] Each total includes fish which were not sexed.

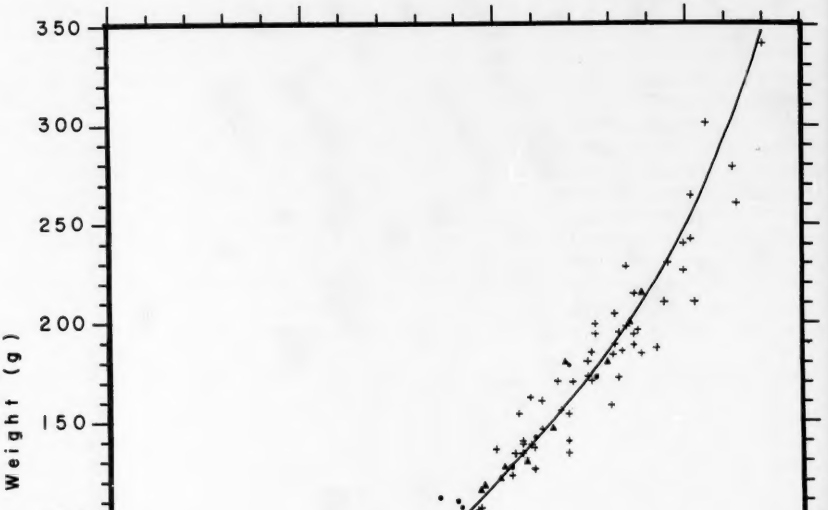

Fig. 3. Plot of weight (g.) and total length (mm.) of *Trematomus bernacchii*. Dots, males; crosses, females; triangles, sex not determined (mostly immature).

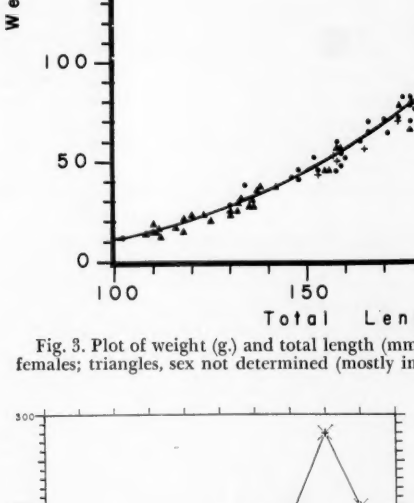

Fig. 4. Plot of average weights (g.) and annulus class of male (dots) and female (crosses) *Trematomus bernacchii*. Average weights, including fish whose sex was not determined, indicated by diagonal crosses.

have a regression with a value slightly less than 3.3894.

A comparison of the average weights at each annulus class for males and females shows clearly that the females live longer and grow larger than the males (Fig. 4 and Table I). Especially noteworthy is the drop in average weight for both the oldest male and female classes.

Similarly, the lengths for female *T. bernacchii* tend to be greater at given ages (Fig. 5). In this figure are also published data of Olsen (1954, 1955) for two related South Georgian species, which occur in somewhat warmer waters. Growth lines of Fig. 5 are arbitrarily drawn.

Discussion

In studies where seasonal markings on scales, otoliths, or other hard parts of fishes

have been extensively examined for determination of age and growth, it has usually been possible to verify the assumptions necessary to relate the growth of the hard parts to the growth of many freshwater and marine species, especially those in temperate waters. Van Oosten (1923, 1929), Hile (1941), and later workers have examined in detail the assumptions necessary to assess growth in this manner. Cooper (1951) notes that "difficult" scales from *Salvelinus fontinalis* growing slowly in cold habitats can be related to seasonal fish growth if care is taken to determine time of formation of first scales and the time when seasonal changes in growth rate are regular enough to result in annulus formation. Even for arctic species where growing seasons are very short, scale annuli may be quite clearly defined, although during the first year of life scales may not be formed or developed sufficiently to give evidence of an annulus (Cohen, 1954). The scale growth and fish growth relationships for older fish can be verified only by studies on fish of known ages or by following growth of marked wild fish from time of release to time of capture; however, this procedure is presently infeasible at McMurdo Sound. The utility of scale growth and aging procedures for a slow-growing arctic species has been verified by the scale studies on individual specimens recaptured after two years (Wohlschlag, 1956).

The assumption of linear growth of both fish and scales would appear to be justified from the plot of data in Fig. 2, with due allowances for sex and sexual maturity differences. The regressions of body length on scale length have intercepts from 34 to 44 millimeters, which suggests the possibility that the length at scale formation is close to this size range. Cohen (1954) found that the calculated lengths at time of scale formation of two similarly slow-growing species agreed with direct observations on fry whose scales formed at age I when they were about 50–60 mm long. From the discussion below it would appear that the number of annual rings plus two would be the actual age of the fish so that the length data of Fig. 5 could also be extrapolated to age I at scale formation and indicate a length at scale formation of about 40 to 50 mm.

While the data of Table 1 confirm the uniformity of increase in scale radii from growth ring to growth ring and suggest that the rings are laid down annually, several

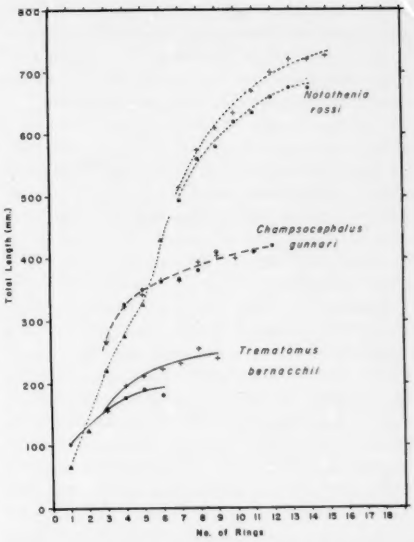

Fig. 5. Comparisons of lengths at different ages of McMurdo Sound *Trematomus bernacchii* with South Georgian *Notothenia rossii* (Olsen, 1954) and *Champsocephalus gunnari* (Olsen, 1955). Dots, males; crosses, females; triangles, immature *N. rossi*.

discrepancies from a direct scale radius-age relationship appear. First, the average radius to the last ring tends to be of the same order as the average total scale radius of the next younger ring class. For example, the scales of the 34 fish with three rings have an average radius of 68.1 mm (times 40) to the third ring and a total radius of 87.0 mm, which corresponds to the average radius of 87.3 mm to the fourth ring of the 32 fish whose scales have four rings. This discrepancy appears to hold in a general way for each of the successive ring (or age) pairings. In spite of repeated observations by three workers, an extra final ring could not be delineated near the margins of the scales. Although the fish were taken mostly during December and January, well after the suspected initiation of austral summer growth in October or November, the "cutting over" of the new circuli apparently cannot be positively distinguished near the antero-lateral margins until later when several more definite completed circuli (without "cutting over") have been established. Such a growth pattern contrasts with arctic fish (Cohen, 1954; Wohlschlag MS) and at least some cold-

water temperate species (Cooper, 1951) in which the beginning of seasonal growth is sharply delineated on the scale pattern. Perhaps the most likely explanation of the arctic-antarctic difference is that growth in the arctic species so far studied occurs when the water temperatures rise several degrees, whereas in the antarctic *T. bernacchii* habitat under consideration, the temperature remains near −1.9° C throughout the year and seasonal growth must be initiated by factors other than temperature. Under the latter conditions it is not unlikely that a substantial portion of a growing season would be required for the formation of a complete scale annulus and for the recognition of the annulus formed the previous season. Due to treacherous ice conditions at time of breakup in late February until strong ice cover forms by April or May, it has been impossible to obtain specimens for growth studies at the end of the summer season and to ascertain when the last-formed annulus can first be clearly recognized. However, specimens taken in midwinter darkness do have a scale pattern (Fig. 1) in which the termination of penultimate summer's growth is clearly defined. For these reasons, it is probably sufficient to add one more year to the number of rings in Table 1 and the figures in this paper.

The second discrepancy from a direct scale radius-growth relationship involves what is known as Lee's Phenomenon (Lee, 1912) whereby the radius to the earlier formed rings tend to be less for the older fish. Except for the average radii to the first ring, the average radii to the second and subsequent rings decrease quite regularly with increasing age as indicated in the vertical columns of Table 1. There is no evidence to substantiate a selective sampling of only the slower growing older members of the population since the largest fish are of the same general size range whether taken by hook and line or by several kinds of traps in McMurdo Sound or by the wide range of gear, including trawls, used to take the fish studied by Norman (1938) and earlier systematists. That mortality tends to be higher for fast-growing members of a population is a reasonable explanation for the phenomenon has recently been discussed by Gerking (1957). In support of this explanation, it should be pointed out that both the oldest males and females are smaller than the next oldest respective age groups (Figs. 4 and 5). Repeated observations on the scales of the two oldest male and female age groups firmly verified this fact.

The frequencies of fish of the different age groups in Table 1 may also be used to estimate annual survival rates on the assumption that the older fish, say those with five or more rings, are sampled in proportion to their true population numbers. For fish with five and more rings a weighted average annual survival rate would be $(31 + 13 + 4 + 2)/(44 + 31 + 13 + 4) = 0.54$. For fish with six and more rings the annual survival would be $(13 + 4 + 2)/(31 + 13 + 4) = 0.40$ which pertains to 35 females, 2 males, and 13 of undetermined sex. These data indicate a fairly high mortality rate increasing with age. Considering the extensive predation by the large Weddell seal the figures are not unreasonable. The data also bear out Gerking's (1957) thesis that unexploited fish species tend to have increasing age-specific mortality rates, with better survival generally exhibited by females.

Since there is a difference in abundance and in survival of the two sexes, it is useful to examine the two sexes for any growth dimorphism which might be reflected in scale growth patterns. Data of Fig. 3 and the weight-length regressions indicate that body form is relatively uniform for all fish and that the fish become relatively deep-bodied with increase in size. It should be pointed out that the gonad development, which tends to make females relatively heavier than males, had not progressed to spawning stages when these specimens were taken. Limited data at present suggest that *T. bernacchii* spawns after the austral summer at which time there may be expected a major difference in the weight-length regressions, judging by the relative difference in size of ripening male and female gonads during midsummer.

The data of Table 1 and Fig. 4 based on observations of gonads suggest that sexual maturity probably begins to occur for most fish about the age represented by three rings, or five years, if the above interpretation of annual scale growth is acceptable. In Fig. 4 the diagonal crosses representing averages of all fish are below the average of the males and females until about the age represented by five rings. From the average weights at different ages it is rather definite that through the age of four rings the larger fish, both male and female, mature earlier.

The fact that the two nine-ring females are smaller than the four eight-ring females

and the two six-ring males are smaller than the 14 five-ring males is illustrated in Figs. 4 and 5. Unless there is some unknown and subtle nonrandom sampling selection it is not too likely that such a condition would arise by chance for both males and females. Olsen's (1955) data also show that there is little or no growth during the last several age classes of *Chaenocephalus aceratus* males and females. Tentatively the best explanation may be, as suggested above, that the slowest growing fish survive the longest. Evidence of size-specific or age-specific mortality would be most obvious in unexploited populations such as exist in McMurdo Sound.

If size-specific mortality exists in a population it would be necessary to modify somewhat the von Bertalanffy (1938) concept of asymptotic size at infinite age as applied in modern fishery exploitation theory (Beverton and Holt, 1957). Also, if growth occurs in "stanzas" depending upon life history stages, a single expression of growth rate becomes inadequate. Actually, *T. bernacchii* and the South Georgian fishes (Fig. 5) seem to show the possibility of three stanzas: (1) up to sexual maturity, (2) sexual maturity to old age and differing between sexes, and (3) old age and differing between sexes. Parker and Larkin (1959) discuss the necessity of describing separate growth increments for growth stanzas and sexes when different mortality rates apply to various life history groups.

A comparison of the growth of *T. bernacchii* living almost continuously at −1.9° C with South Georgian species (Olsen, 1954, 1955) at the edge of the antarctic ice pack limits where temperatures are above 0° much of the year (U. S. Navy, 1957) shows that the growth in these slightly warmer and biologically richer waters, allowing for specific differences, is much greater (Fig. 5). The growth rates of both whitefish (Cohen, 1954) and herring (Wohlschlag, MS) in Alaskan inshore arctic marine waters, whose temperature may reach 10° C for a short period during approximately two or three months of open conditions, are about the same order as that of the McMurdo Sound *T. bernacchii*. The comparison of growth rates of these cold stenotherms assumes a special physiological importance in relation to cold adaptation (Wohlschlag, 1960) and possibly to efficiencies of transformation of food energy to growth. Judging from scale growth patterns the arctic fish grow almost entirely during the warmer period when their metabolism is much higher than the remainder of the year. Yet *T. bernacchii* at −1.9° C has a metabolic rate but slightly lower than the arctic forms at above-freezing summer temperatures, and still its growth rate is about the same.

It is known that a slight rise in temperature has a much greater effect in increasing metabolism of the temperate *Lepomis macrochirus* adapted at wintertime temperatures than at other warmer seasons (Wohlschlag and Juliano, 1959). Data of Scholander *et al.* (1953) and Wohlschlag (1957) indicate that the summertime growing season temperature-metabolism coefficients of arctic species may be lower than the summertime growing season coefficient of the *T. bernacchii* (Wohlschlag, 1960). It is quite possible that a similarly high temperature-metabolism coefficient with higher temperatures, longer growing season, and adequate food supplies could account for the relatively phenomenal growth of the more nearly subantarctic South Georgian species, even though both *Champsocephalus gunnari* and *Chaenocephalus aceratus* studied by Olsen (1955) have no respiratory pigment.

Summary

To determine the nature of fish growth under almost permanent sea ice cover and at constant freezing temperatures throughout the year, studies were conducted on *Trematomus bernacchii*, a common notothenid bottom fish from McMurdo Sound, Antarctica.

Scales from this species have rings which can be interpreted as annuli. It is likely that scales, and hence annuli, are not formed during the first year and until the fish attains a length of around 40 millimeters. Due to the gradual cessation and resumption of summer growth, the last annulus near the outer margin cannot ordinarily be identified. Thus the actual age is most likely the number of annual growth rings observed plus two.

Radii to the various annuli suggest that older and larger fish grow more slowly than the younger and smaller fish (Lee's Phenomenon).

Survival rates tend to decrease with age. Females survive longer than males.

Males and females tend to have uniform morphology with respect to weight-length regressions. For all fish, the regression of

weight in grams on total length in millimeters is:

log weight = −5.6519 + 3.3577 log length.

Females tend to be larger than males after both are sexually mature at about five years. There is a suggestion that both the oldest males and females may be somewhat smaller than those at penultimate ages.

The relatively high growth rate of *Trematomus bernacchii* at freezing temperatures is discussed with reference to cold adaptation and temperature-metabolism coefficients.

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Department of Biological Sciences, Stanford University, Stanford, California.

Observations on the Natural History of the Mud-skipper, *Periophthalmus sobrinus*

Robert C. Stebbins and Margaret Kalk

In April, July, and December, 1959, and February, 1960, an opportunity was afforded us to study the mud-skipper, *Periophthalmus sobrinus* Eggert, on Inhaca Island, 20 miles east of Lourenço Marques, Portuguese East Africa. Captive individuals, transported in mud and water from their habitat to the University of the Witwatersrand, Johannesburg, were kept under observation in a terrarium in the laboratory. Stebbins, with interests in the temperature of cold-blooded animals, focused attention on thermal characteristics and behavior. Kalk, familiar with the ecology of the Island (Macnae and Kalk, 1958), emphasized habitat features and food habits. Although our field work has not been extensive, it is hoped this preliminary study will be the stimulus for further work on *Periophthalmus* on Inhaca Island.

A number of papers have been published on the anatomy, respiration and behavior of various species of *Periophthalmus* (see litera-

ture cited), the latter frequently under terrarium conditions, but field studies are scant. Although some of our observations duplicate previous ones, such reinforcement does not seem undesirable.

The field work in April was done during a period of low spring tides on the mangrove-bordered sand flats of a sheltered bay, approximately one mile east of the laboratory, Estação da Biologia Maritima, which is situated on the west shore of the Island. The technique employed by herpetologists in obtaining body temperatures of reptiles and amphibians by means of a quick-recording mercury thermometer inserted into the vent was applied successfully to the fish. In order to obtain the temperature quickly and with a minimum of pursuit and handling, the mud-skippers were stunned by shooting them at close range (2 to 3 feet) with rubber bands cut from automobile-tire inner tubes and fired from the thumb. This method was found to be more successful than shooting with .22 caliber dust shot. Best catches were obtained when the fishes were fully out of the water against firm mud that yielded little under the impact of the band. The entire band left the thumb, and itself served as the missile. The stunned fish was lightly held by the head to steady it as the thermometer bulb was inserted. In some individuals considerable force was required to penetrate the small anal opening and some bleeding occurred. The fish was measured and sexed on the spot and preserved in formalin for study of stomach contents. Analysis of the movements of the fins in locomotion on land was aided by motion pictures and study of tracks made in mud.

The range in size (total length) of mature females was 61.9 to 90.0 (mean 76.6) mm. and of males was 58.2 to 85.2 (mean 74.8) mm. Many smaller individuals, about 40 mm. in length, which had apparently metamorphosed recently, were also seen but not studied. The adults were smaller than the average reported by Smith (1959) for the Indo-Pacific Ocean populations.

Habitat

The fish were found in close association with the dense mangrove border of the tidal sand flats. They occurred within the mangroves along tidal channels that connect the open area of the high spring-tide zone with the low-tide flats. The banks of these channels are lined with the arching buttress roots of the mangle, *Rhizophora mucronata*. The fish were especially numerous among the pneumatophores of *Avicennia marina* along the seaward fringe of the mangroves where the tidal channels opened out onto the flats. They were common in well-illuminated areas that adjoined the shade of the trees, chiefly on dark muddy sand, rich in organic content. One individual was seen near the high-tide mark in water over a substratum of nearly clean sand.

With the incoming tide, individuals moved along the tidal channels from the mid-tide areas and dispersed into the high-tide zone, as did gobies (*Ctenogobius nebulosa*), bull's eye fish (*Therapon theraps*), the glassy (*Ambassis safgha*), pipefish (*Syngnathus* sp.), penaeid prawns and swimming crabs (*Thalamita* sp.). As the tide ebbed, a return movement occurred. Such migratory individuals may have two foraging areas connected by a tide channel; one in the mid-tide area and the other in the high-tide zone. In the winter period of study (July) it was fairly certain that the fish returned to their mud nests at night since they were found within the nests in the early morning when the tide had just receded, unless the sun had been shining directly on the nest. Migration with the incoming tide in the afternoons was not seen but was common in December and April.

Most of our work was done in the mid-tide zone around the mouths of the tide channels. Here the surface was nearly level, and, when the tide was out, the shallow channels carried a gentle flow of water that drained from the mangrove area to the sand flats. In one representative area the water of the channel was 1 to 2 feet wide and ½ to several inches deep at low tide. The adjoining open expanse of fairly soft mud was riddled with burrows of fiddler crabs (*Uca annulipes, U. chlorophthalmus* and *U. urvillei*), marsh crabs (mainly *Sesarma guttata*), pistol shrimps (*Alpheus crassimanus*) and swimming crabs (*Thalamita crenata*). The flatter parts had become a mass of shallow pits filled with tide water, some of which may have been the broken-down or abandoned nests of *Periophthalmus*. These pits frequently contained burrows below the surface of the water, which were sought as places of refuge by the mud-skippers. Pneumatophores of *Avicennia*, unbranched vertical roots 3 to 6 inches in height were irregularly present over the entire area. They frequently bore barnacles (*Balanus amphitrite*).

At another site, the mud-skippers were abundant on the sunny, gently sloping bank of a tidal channel that at low tide was 6 feet across and 1½ feet deep. *Rhizophora mucro-*

nata with buttress roots fringed the banks. On one side the trees were 12 to 15 feet from the water's edge, whereas on the east bank their roots entered the water. The fish were most common in the open, well-illuminated area.

Territorial Behavior and Nesting

Adults were abundant during peaks of surface activity, perhaps averaging one individual every 10 to 15 feet. They tended to be solitary, but occasionally close associations occurred.

Along a mud beach in a salt evaporation basin on the west bank of the Matola River, 3 miles southwest of Lourenço Marques, we watched eight adults and one juvenile foraging along a 6 to 8 foot strip of beach. The fish seldom went more than a foot away from the water's edge. Within this area they tended to space themselves and maintain territories, but chases were common, the larger individuals pursuing the smaller ones. The juvenile was pursued most of all. Once on the close approach of another individual, a large adult elevated the dorsal fin. The black, white and orange markings of the fin, suddenly displayed, may have served as a warning. The same flicking response was often seen along a tidal channel on Inhaca Island where some 10 individuals were crowded into an area 90 to 100 square feet in extent. Approaching individuals were often smaller than the displaying ones Many encounters and pursuits were seen in which no fin action occurred.

Spacing was also evident in the distribution of nests (Fig. 1C). Along a shallow tide channel in an uncanopied area 6 x 13 yards, bordered by *Avicennia* and *Rhizophora* trees, we found 21 nests. They were spaced approximately 4 feet apart with extremes at 2½ and 6 feet. The nests bordering the channel were all about 2 feet from the water's edge. The area was nearly level, and pneumatophores of *Avicennia* were numerous. Here and at other sites where we found nests there was shade during part of the day, and some of the nests were in the shade all day. The fish seems to choose shadier places for nests than those ordinarily sought for foraging. It was impossible to tell whether all the nests were in use. Individuals caught in nests were females, but no eggs or fry were seen in April. In some the chimneys seemed to have been partly eroded away by tide action, and others were nearly level with the ground. It is possible that these were the breeding nests of the previous season which, for the species in Sumatra, were considered by Harms (1935) as being more elaborate than the between-season ordinary nests. In July there were many nests marked only by two openings in the ground that led into a common chamber. These were inhabited by small single individuals, while the turreted nests often contained larger pairs.

Numbers of juveniles 3 to 5 cm. in total length were seen in areas of mixed light and shade beneath the mangrove canopy near the nests. Presumably, as in mud-skippers studied by Harms (1935), they metamorphosed from aquatic larvae.

We opened a number of nests and found that while they were similar in structure to those of other species (Harms, 1935 and Champeau, 1951), they differed in details. The cavity of the nest is Y-shaped with the brood-chamber below and the arms as paired entryways (Fig. 1A). Chimneys of mud, one usually higher than the other, are built as the tunnels are extended upwards. The chimneys are formed of pellets of mud carried in the mouth from the interior to the openings of the nest and ejected like toothpaste from a tube (Fig. 1B). We saw an adult female at the mouth of the burrow with a small blob of mud on her snout and traces of mud in the mouth. She had apparently recently deposited a mud pellet. We watched this individual for over an hour during which time, perhaps influenced by our presence, she remained in the nest tunnel without replenishing her supply of branchial water. The gular region was immobile and drawn inward. The nearest water was some 20 feet away, and there was none in the chamber of the nest. The body temperature of this individual was 24.6°C.

The bases of the nests were about 10 to 20 inches below the general surface of the ground, and the point of junction of the arms of the Y about 2 to 4 inches below the surface. Chimneys were 1 to 3 inches high and the distance separating the two openings 3 to 4 inches. The external openings were ⅜ to ¾ of an inch in diameter but the tunnels enlarged toward the main chamber. The nest cavities in most instances were connected to the surface by one or more tunnels other than the usual ones, perhaps burrows made by other animals. In one case the fiddler crab *Uca chlorophthalmus* had made a small burrow in the chimney of a nest. One nest had a third tunnel joining at the junction of the arms of the Y. A total of 25 nests was explored.

Of the adult fishes captured, 29 were males and 21 females. Four of the females examined in April had much enlarged ovaries, yellow

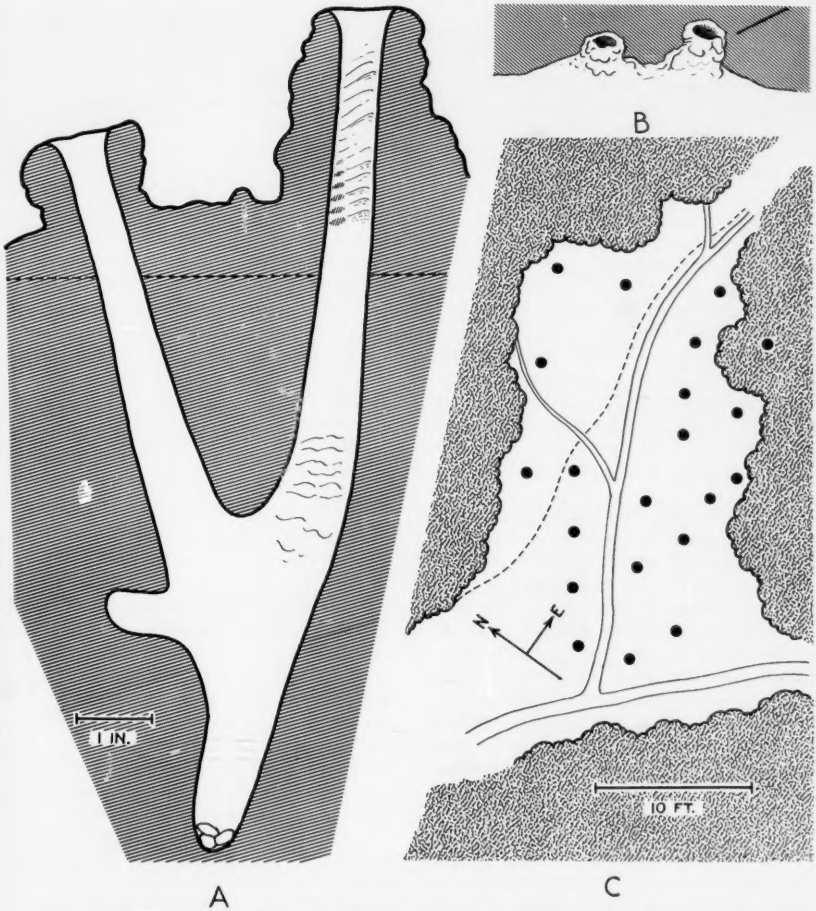

Fig. 1. A. Vertical section of the nest of the mud-skipper (*Periophthalmus sobrinus*) based on direct tracing of the outline of a nest. Lines in the upper part of the right tunnel represent impressions in the mud wall of the nest made by the left pectoral fin; "elbow" marks show at the lower left, impressions of the fin rays at the right. The horizontal line indicates the general level of the surface of the ground. Several pellets of mud lie in the bottom of the nest. B. Nest chimneys. They are usually of unequal height. Note pellets of mud that compose the walls. C. Distribution of nests (solid black circles) in exposed patch of mud flat surrounded by mangroves. Note regular spacing of nests. At low tide water stood in the tide channels as indicated by branching lines. The broken line represents the edge of a shaded area present at the time of our visit (April 10, 1959, 3:45 p.m.).

orange in color and containing mature eggs. No trace of ovoviviparity, described for other species of *Periophthalmus* (Harms, 1935), was seen at any time. Lack of synchrony in individual breeding cycles seemed evident on all visits.

We found we could distinguish sex externally by the shape of the anal papilla which projects posteriorly from the rear margin of the vent. In males the papilla is more elongate, less truncate, and more tapered distally than in the female. Its distal end in the female tends to be bilobed, whereas in the male it is smoothly rounded. In occasional individuals of both sexes some brown pigment may be present toward the tip. In one male the palp was divided into a pair of finger-like structures.

Feeding

On Inhaca Island we found *Periophthalmus* feeding on small animals, often only a mm. or so in length, on the surface and in the mud, as reported for other species by Harms (1929) and Champeau (1951). It detects its food chiefly, if not entirely, by sight. All feeding observed by us occurred in well-illuminated areas where glistening wet surfaces might be expected to produce a dazzle effect. Walls (1942) has pointed out that the retina is rich in cones. The lower half is pure cone, and the upper half has an area composed entirely of rods along the extreme superior periphery. When the eye is viewed from the side and illuminated from above, nearly the entire pupil appears bronze, grading into blue green and thence into indigo blue in the lower part. The colors quickly vanish when the eye is rotated away from the observer or on puncturing the eye ball, which indicates a structural effect.

The eyes are raised in "conning towers" and can be retracted into sockets below. According to Walls (from Karsten, 1923), the spectacled cornea is curved, but the spherical lens is slightly flattened on one side so that sight is normal or slightly hypermetropic in air. It is to be expected that the eyes would be adapted for vision at close range, but these fish also see well at a considerable distance. They showed alarm when we were at a distance of 30 feet, but soon became accustomed to our presence if movements were restrained. It has also been reported that *Periophthalmus* can hear vibrations up to 651 cycles per second (Diesselhorst, 1938).

We spent many hours watching feeding. The foraging animal alternates forward movements with periods of quiescence. A pounce for food can sometimes be anticipated because of the attentive, immobile attitude that precedes the leap, the fish no doubt intently watching its prey. We seldom saw the prey, indeed it can rarely be discerned on the surface of the mud, even with a lens. The fish may have often been responding to slight surface movements of partly buried small animals, that could not be detected by us at a distance of 6 to 8 feet separating us from the fish. The pounce was made to the front or sometimes to the side and consisted of a sudden lunge forward and downward, the snout usually disappearing in the mud and the tail tipping up in the air. Perhaps the papillae on the upper lip, in which the ventral openings of the nasal sacs occur, may have a tactile or olfactory function in detecting prey in the mud when the snout is buried and the eyes can be of little use. The turret-like position of the eyes, high on the head gives the animal visual scope in all directions.

The act of feeding is accompanied by expulsion of the air and water from the branchial chambers and is followed by movement to a nearby pool for a refill, as described later.

We have found the following animals in the stomach contents: the polychaetes, *Polydora* and *Dendronereis arborifera* and an occasional terebellid; nematodes; crustaceans, including copepods, tanaids, schizopod larvae of prawns, juveniles alpheid shrimps, megalopa larvae of crabs, juvenile of the shade-loving species of fiddler crab, *Uca chlorophthalmus*, the small sand crab, *Dotilla fenestrata* and, in July, very small mud shrimps (*Upogebia*) and larvae of ephydrid flies. A certain amount of sand and plant debris was found in all guts examined.

Locomotion

Inger (1952) and van Dijk (1959) have described locomotion on land, and van Dijk illustrates the track made on smoked paper. In crawling forward the pectoral fins are moved in a fore and aft direction. They are simultaneously lifted well off the substratum while the body is supported by the pelvic fins which are attached just behind the pectorals to the pectoral girdle (Lele and Kulkarni, 1939). The tip of the pectoral describes an arc as it moves forward to initiate a locomotor movement. The tip of the fin is placed against the substratum somewhat in advance of the level of the opercular opening but behind the eyes. In soft mud, marks indicate some lost motion before the tip obtains sufficient purchase to propel the body forward. Toward the end of the backward stroke, the pelvic fins may be seen moving forward while the body is held well off the substratum by the pectorals. The pelvics contact the ground and exert some backward pressure (as evidenced by track impressions in mud, Fig. 2J) as the pectorals conclude their backward motion and swing forward for the next stroke.

When crawling, the body is held well off the ground anteriorly but is in contact with the ground posteriorly at the level of the anal fin. A narrow drag mark is made by the base of the tail, indicating a minimum of friction from this inert part of the body. The tailfin is folded and the tip of the tail is directed upward, thereby reducing the area of contact with the ground.

When moving rapidly, a seal-like movement

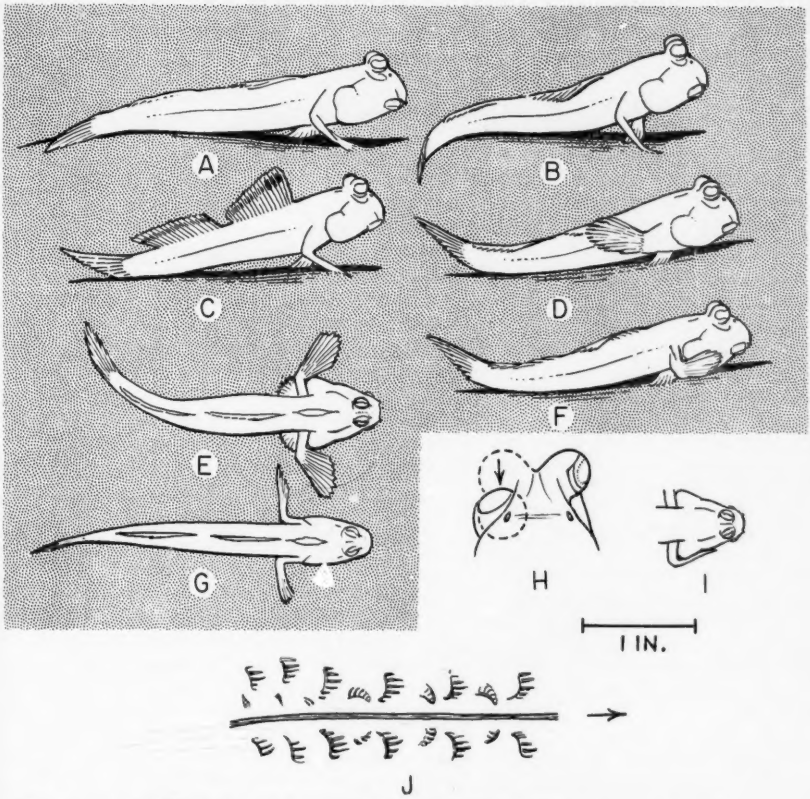

Fig. 2. (A to F) Sketches of poses assumed by captive mud-skipper (*Periophthalmus sobrinus*). (A and B) Attentive pose assumed during pauses in crawling forward. (B) Watching for prey; head held high. (C) Fin display on close approach of another individual. (D, F, and I) Stroking action of pectoral fin on buccopharyngeal region (see text). (E) Branchial cavities filled with air and water. (G) Appearance after expulsion of air and water. (H) Direction of movement of the eye when depressed into socket. Note the loose fold of skin that acts like a nictating membrane. (J) Track in soft mud. Arrow indicates direction of movement. One inch scale applies to all illustrations except H and J.

of the posterior part of the body is used to propel the fish forward by a series of leaps. The tail is curled to one side and firmly placed against the substratum, the anal fin perhaps helping to prevent slipping. The body loop is then straightened as the fish pushes off with its pectorals. A jump of 1 or 2 feet may occur, with the fish rising to a height of a foot or so in the air. When several jumps are taken in rapid succession, the animal may quickly move away from a person walking toward it.

Periophthalmus usually swims submerged with the normal motions of a typical fish, but individuals startled into the water may swim at the surface with the head out, apparently because of the bouyancy of the air-filled buccopharyngeal region. Although some individuals remained submerged for 10 minutes or more, most skittered across to the opposite side of a pool or tidal channel. This action somewhat resembles a ricocheting stone, and the fish strikes the surface at an acute angle. The rebound from the surface is probably reinforced by tail action, and the animal is launched into the air. Motion pictures reveal that the dorsal fins are elevated, sail-like, probably providing stability and helping to prevent rotation of the body in the air. The fish can cover 2 to 4 feet at a jump and rise 6 to 12 inches above the surface.

Respiration

Respiration and anatomical features of the branchial cavity in *Periophthalmus papilio* have been described by Willem and Boelaert (1937), who have adequately dismissed the suggestion of Haddon (1889) and Hickson (1889:30) that the tail is an important respiratory organ. However, our observations on the mechanism of breathing do not correspond in every particular with theirs.

When *Periophthalmus* is submerged, rhythmic opercular movements occur as water is drawn in through the mouth and passed out through the opercular openings, in the usual manner of fish and aquatic larvae of amphibians. An individual resting on the bottom of an aquarium stirred up small clouds of silt to the rear of the opercular openings as water was expelled. In our animals, the usual mode of underwater respiration did not involve use of air trapped in the branchial cavity, as suggested by Willem and Boelaert (1937).

When the fish comes out on land, it commonly pauses at the water's edge and gulps air. This involves a quick distension of the branchial cavity (Fig. 2E). The small valvular opercular openings are closed, and with a quantity of water held in the gill chambers, as well as the trapped air, oxygen-rich water is available for gill respiration on land. The branchial region remains distended and opercular movements are suspended. When feeding, the fish makes a sudden lunge to seize its prey and simultaneously expells the air and water, forcefully and audibly, through the opercular openings, wet patches or bubbles appearing on the surface of partly dried mud. The sound can be heard at a distance of 15 to 20 feet. The fish then crawls promptly to a nearby puddle or tide channel, replenishes the water in its branchial cavity by means of a few seconds of rapid pumping with the mouth under water and once again gulps air at the surface, distending the opercular region. We observed feeding many times, and the pattern was the same. Expulsion of water and air also occurred in captive animals in the absence of feeding. Gulping and distension of the branchial cavity with water was seen in a submerged *Periophthalmus,* a movement different from that of normal respiration under water. This individual appeared to be attempting to flush out the branchial cavity to remove some ink which had entered the gill chambers in the course of an experiment designed to record its tracks.

It seems evident that any movement that might cause mixing of the air and water in the branchial chambers would improve oxygenation of the trapped water. We saw two actions that may have directly (or perhaps incidentally) served this end. Frequently, following replenishment of the branchial cavity with water and air after feeding, and occasionally at other times, the fish rolled over on one side or the other, sometimes on both sides in rapid sequence. This happened both on land and in shallow water when the fish was only partly submerged. At first we thought it was a method of cleaning the eyes following feeding, since often the head was buried nearly to the eyes when prey was sought in soft mud, and the face became spattered with mud. However, since it was seen in captive non-feeding individuals that rested on wet sacking, the foregoing interpretation did not seem adequate. Perhaps the movement ensures that the gills are thoroughly wetted and at the same time helps to mix the water and air in the branchial cavity. With the head held in the usual nearly horizonal position, adequate wetting of the dorsal part of the gills may depend on capillarity and body rotation.

The other action which may have a respiratory function is the head stroking movement of the pectoral fins. This is seen in terrestrial individuals that have come to rest on the pelvic fins and tail, thus freeing the pectoral fins temporarily from their role in support and locomotion. The pectoral on one or the other side, sometimes alternately, is brought forward from a resting position against the side of the body (Fig. 2D, F and I) to the side of the head over the pliable part of the operculum. The upper border of the fin may be held slightly away from the opercle while the rest of the fin executes a gentle upward stroke. The fin is then returned to its original position or extended laterally. Since the tissues around the opercular edge are soft, it is thought that this movement, by deformation of the branchial cavity, may help to mix air and water.

We observed this action in isolated fish, which tends to rule out the possibility that it serves as some form of signal between individuals. The movement appears to be too stereotyped and regular to be a scratching response as mentioned by Champeau (1951). There is also the possibility that the muscular movements of this action may contribute to mixture of the branchial air and water. Indeed, the normal locomotory movements may have an important part to play here, but we have not had opportunity to investigate this.

Willem and Boelaert (1937) reported that

rhythmic retraction of the eyes into their orbits depresses the ceiling of the buccal cavity so as to compress and mix the air and water in the branchial chambers. This interpretation of the eye movements would not appear to apply to our animals, since forceful depression of the eyes of freshly killed fish caused no appreciable depression of the buccal roof. Considerable force had to be applied to obtain any deformation whatever. The eye movement probably serves to clean the eye surfaces and, on land, perhaps to moisten them with residual water that may be present in the depression below the eyeball. The movement was also seen in submerged individuals. As the eye is depressed, a loose fold of skin below the eyeball sweeps over the eye (Fig. 2H).

In addition, the rather extensive fin surfaces and the skin (particularly on the head) which are well vascularized (Schöttle, 1931), supplement gill respiration, both in water and on land. Diverticula of the nasal sacs are probably also important (Harms, 1929).

The idea that caudal respiration is of special importance is based chiefly on the habit of these fishes of occasionally resting with the foreparts out of the water and tail submerged, and not on morphological or sound experimental evidence. It seems doubtful to us that the tail is more important than other fin surfaces in supplementing respiration. When the animal is active out of water, the caudal fin is frequently folded. Both on land and in water the gills appear to be the chief respiratory organs. We did not observe the synchronisation of caudal and branchial respiratory movements in submerged fish, reported as occasional by Willem and Boelaert (1937).

Three individuals were tested in February, as to their tolerance of submersion. They were placed in a net-covered aquarium 12 inches square, submerged in a tank of circulating sea water. This ensured that the oxygen content of the water did not fall below 4 ppt. The animals were in good condition after 3½ days, when the experiment had to be terminated. They showed no signs of distress. Periodically they swam to the net cover in attempts to get out.

When the fish were submerged singly in about a litre of water, attempts to reach the surface occurred after about 20 minutes. Thereafter, at intervals of about 5 to 20 minutes, they swam rapidly to the top of the jar and then descended again. When deprived of surface air for 3 to 4 hours, they ceased breathing and became inert, but they recovered when promptly removed. Gobies (*Ctenogobius nebulosa*) of the same size, in the same volume of water, succumbed to asphyxiation in 3 to 4 hours. They are not known to be air breathers and usually do not surface when kept in a large aquarium. It was concluded, therefore, that the mud-skippers were immobilized because of anoxia.

Although it is common to see them skipping from mangrove branch to bank in a channel at high tide during summer afternoons, in winter at that time they are apparently submerged and in their nests, since they are found in them the next morning. It would seem that their surface activity is in no way related to respiratory difficulties under water but depends rather on the warmth of the sun.

Temperature Characteristics

We studied the temperature responses of *Periophthalmus* from 9:45 AM to 2:37 PM on April 8, 12:00 N to 3:00 PM on the 9th and 11:45 AM to 3:03 PM on the 10th. The span of recorded environmental temperatures available to fish active on the surface during these periods was as follows: water, 25.9° to 35.4°C.; mud surface, 27.1° to 37.1°C.; and air ½ inch above the substratum, 24.6°C. (overcast) to 30.8°C., i.e. approximately a 10°C. range in water and substratum temperatures and a 6°C. range in air temperature. A range of about 10° was also available from a depth of about 1 foot to the surface. Body temperatures of active fishes (17) ranged from 28.7° to 34.4°C. with a mean of 31.5°C., essentially the same as that of the mud and water. This is to be expected because of the close contact of the fish with the mud surface and their frequent excursions through water. They do not allow their skin to dry. The lowest rectal temperatures recorded were 24.6°C. and 25.0°C. in fish ensconced in their mud nests.

Although mud temperatures of 37°C. were recorded, fish were not found in areas where such values prevailed; they seemed to avoid situations which would cause their body temperature to rise above 35°C. A more intensive study might be expected to yield rectal readings higher than those recorded in April, but the agitated behaviour of the fish placed in water at 37 to 38°C. suggests that they are not comfortable at such body temperatures. The critical maximum, i.e. the temperature at which locomotion and respiratory activity ceased was investigated. Five tests were made, and the fish ceased breathing at water temperatures of 40.4°, 41.3°, 41.6°, 42.0° and

42.3°C. All recovered within a few minutes when placed in water at 31°C. The procedure was to stir warm water gradually into the water occupied by the fish. In two individuals slight dorsal flexure of the body occurred, and in all of them the fins were fully extended at the time movements ceased; the skin became light in color with dark vertical bands.

Because of a possible role in thermoregulation it should be mentioned that *Periophthalmus* is capable of color change from pale beige with black to dusky markings and white flecks (guanophores) to sooty with obscure markings. In the dark phase the pale yellow pelvic fins are blackish, with a yellow border. In fish of both sexes the dorsal fins may have considerable orange-red color which fades on preservation.

In exposing themselves to the direct light of the tropical and subtropical midday sun on unshaded mud flats, terrestrial fishes such as *Periophthalmus* probably approach the extreme among fishes in exposure to solar radiation—the heat absorbed under such circumstances is perhaps exceeded only by fishes that inhabit hot springs. *Periophthalmus* does not survive well in captivity if the terrarium temperature is low. On April 9, an overcast, cool day, it was evident that activity in the field was greatly reduced, a reaction to cool weather resembling that of most reptiles. In winter (July) the fishes remained within the turrets at the entrance to the nests until the sun shone directly onto them. The numbers abroad later in the day depended upon the warmth of the weather. Little information was obtained on the critical minimum temperature tolerance, but an individual tested in February was immobilized at 10°C. Iced water was added slowly to the experimental chamber. At 15°C. the posterior dorsal fin was raised and the animal was fairly quiet, but as the temperature fell it engaged in spurts of activity, raised its anterior dorsal fin and finally ceased breathing and became rigid (not flexed) at 10°C. It recovered completely when put in water at 20°C.

Evolution of the Terrestrial Habit

At low tide the mangrove goby (*Ctenogobius nebulosa*) was present in the shallow channels that continued to flow after the tide had receded, and individuals were seen trapped in small pools that formed in the depressions made by various burrowing animals. Some of these isolated pools were far removed from the tide channels. One individual, over 6 inches in length, was found in a pool 1 foot across and about 1½ inches deep. The snout of the fish was above water, but the mouth was just below the surface. Schools of these fish were seen wriggling across shallow portions of the tide channels, their backs out of the water, in the manner of migrating salmon.

Watching these gobies one can readily appreciate the survival value of the terrestrial habit of *Periophthalmus*. In an environment where twice every 24 hours the aquatic habitat is reduced to disconnected pools and narrow channels, chances of a fish being trapped in an exposed location are considerable. Usually when isolated thus, the threat of predation, overheating, suffocation and desiccation would be greatly increased and opportunities for feeding decreased. Under such conditions a premium would be placed on structural and functional changes that would make possible survival on land. Perhaps, as proposed by Romer (1933) for the ancestors of amphibians, an important factor in the evolution of the terrestrial habit of *Periophthalmus* may have been the survival value of locomotion on land in avoiding being trapped in drying pools. Other factors may have been the feeding opportunities on land and avoidance of interspecific competition (Pearse, 1931, 1932, 1933). Inger (1952) thinks feeding opportunities on land were decisive. *Periophthalmus* has freed itself from some of the limitations imposed by the aquatic medium, yet at the same time has retained many of the features of its earlier manner of life.

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A Review of the Tropical Eastern Pacific Species of *Pareques* (Sciaenidae)

J. D. McPHAIL

PAREQUES is a tropical American genus of the family Sciaenidae. Most recent authors (Barton 1947, Hildebrand and Barton, 1949) have not recognized *Pareques* as a distinct genus, and have included it in *Equetus*. Earlier Jordan and Evermann (1898) divided *Equetus* into two subgenera, *Equetus* and *Pareques*. (Jordan and Evermann (1898) used the name *Eques*. Hildebrand and Barton (1949:18) note that *Eques* is preoccupied, and that *Equetus* is the next available name.) Jordan, Evermann and Clark (1930) listed *Pareques* as a separate genus, but presented no reasons for this change. The present study is an attempt to clarify the taxonomic position of *Pareques*, and to review the tropical eastern Pacific species of the genus.

All counts and measurements follow Hubbs and Lagler (1958). Body proportions are calculated. Vertebral counts and other skeletal details were determined from radiographs. Ninety-three specimens from 39 localities were examined. These data are included in redescriptions of the tropical eastern Pacific species. The following abbreviations are used for museum specimens: BC, University of British Columbia; CNHM, Chicago Natural History Museum; SIO, Scripps Institution of Oceanography; UF, University of Florida; USNM, U. S. National Museum; W, University of California at Los Angeles.

Genus *Pareques* Gill

Pareques Gill in Goode, 1875:50 (type species *Grammistes acuminatus* Block and Schneider 1801, by original designation).

Body oblong, compressed, anterior profile steep, back tapering rapidly to a narrow caudal peduncle. Mouth small, inferior, horizontal to slightly oblique. Snout round, blunt, projecting slightly beyond the premaxillaries. Lower jaw with a fleshy symphyseal knob; snout and symphyseal knob with well developed slits and pores. Teeth villiform, in broad bands; outer row in upper jaw somewhat enlarged. Preopercle crenulate, without bony serrae. Scales ctenoid, except below eye and on opercular flap, extending onto the median fins. Gillrakers short, 16 to 22 on the first gill arch. Spinous dorsal short, triangular in outline, with 8 to 12 normally developed spines. Soft dorsal with 36 to 46 rays increasing in height posteriorly. Branchiostegal rays 6 or 7 on either side. Three free interneurals anterior to the first dorsal fin; 25 vertebrae. Anal fin inserted under middle of soft dorsal; second anal spine slightly enlarged. Pyloric caeca short, 6 to 8 in number. Four known species: *Paraques acuminatus* (Bloch and Schneider), *P. viola* (Gilbert), *P. lanfeari* (Barton), and *P. fuscovittatus* (Kendall and Radcliffe).

Generic relationships.—Jordan and Evermann (1898) divided the genus *Equetus* into two subgenera, *Equetus* and *Pareques*. The subgenus *Equetus* was distinguished by XIV to XV–I dorsal spines, and approximately 9 interneurals wedged between the neural spines of the second and third vertebrae. The subgenus *Pareques* was distinguished by X to XII–I dorsal spines, and 4 to 6 interneurals wedged between the neural spines of the second and third vertebrae. Jordan and Evermann placed the species *lanceolatus* in the subgenus *Equetus*, and included the species *acuminatus, viola, punctatus* and *pulcher* in the subgenus *Pareques*. Jordan, Evermann and Clark (1930) retained this grouping of the species.

Equetus (*sensu lato*) is divisible into two distinct groups. However, the division presented by Jordan and Evermann (1898) is unnatural. The species *lanceolatus, punctatus* and *pulcher* form one closely related group, while the species *acuminatus, viola, lanfeari* and *fuscovittatus* form another. The characteristics distinguishing the two groups are: the presence or absence of free interneurals anterior to the first dorsal fin, and the relative development of the first dorsal fin (Fig. 1).

The species *lanceolatus* and *punctatus* have no free interneurals anterior to the first dorsal fin. No specimens of *Equetus pulcher* large enough for positive identification were available for X raying. The first dorsal fin in adult specimens of *lanceolatus, punctatus* and *pulcher* is long and filamentous, and extends more than half-way along the base of the soft dorsal when depressed. The species *acuminatus, viola, lanfeari* and *fuscovittatus* have 3 interneurals anterior to the first dorsal fin. The first dorsal fin in these species is not long and filamentous, and extends only to the base of the first few rays of the soft dorsal when depressed.

The characteristics separating these two groups of species are constant. There were no intermediates among the specimens examined. For this reason *Equetus* and *Pareques* are considered distinct genera.

Jordan and Eigenmann (1889:440) considered *Equetus* (*sensu lato*) to be closely related to the ill-defined genus *Sciaena*. The following species of *Sciaena* were examined: *Sciaena deliciosa* (Tschudi), *Sciaena saturna* (Girard), and *Sciaena fasciata* (Tschudi). Many authors place the species *saturna* and *fasciata* in a separate genus *Cheiliotrema* Tschudi. *Sciaena* has three heavily ossified interneurals anterior to the spinous dorsal. In this characteristic, and in general body shape, *Pareques* is closer to *Sciaena* (particularly to those species sometimes placed in *Cheiliotrema*) than to *Equetus*.

Key to the Tropical Eastern Pacific Species of *Pareques*

A. Soft dorsal with 38 to 46 rays. Body with or without longitudinal dark stripes. Stripes if present, 6 to 9 and extending onto the head.

  B. Spinous dorsal with a wide white margin on the posterior edge; soft dorsal and caudal with a narrow white margin. Body with stripes, the first dorsal stripe curved abruptly downward below the spinous dorsal. Chacala, Nayarit to Acapulco, Guerrero, Mexico. . *Pareques fuscovittatus* (Kendall and Radcliffe).

  BB. Spinous dorsal without a distinct white margin on the posterior edge; soft dorsal and caudal without a narrow white margin. Body with or without stripes; if stripes are present the first dorsal stripe is not curved downward below the spinous dorsal. Point Eugenio, Baja California, Mexico to Cabo Blanco, Peru. . . . . *Pareques viola* (Gilbert).

AA. Soft dorsal with 35 to 37 rays. Body with 4 longitudinal dark stripes which never extend onto the head. Talara to Chimbote, Peru. . . *Pareques lanfeari* (Barton).

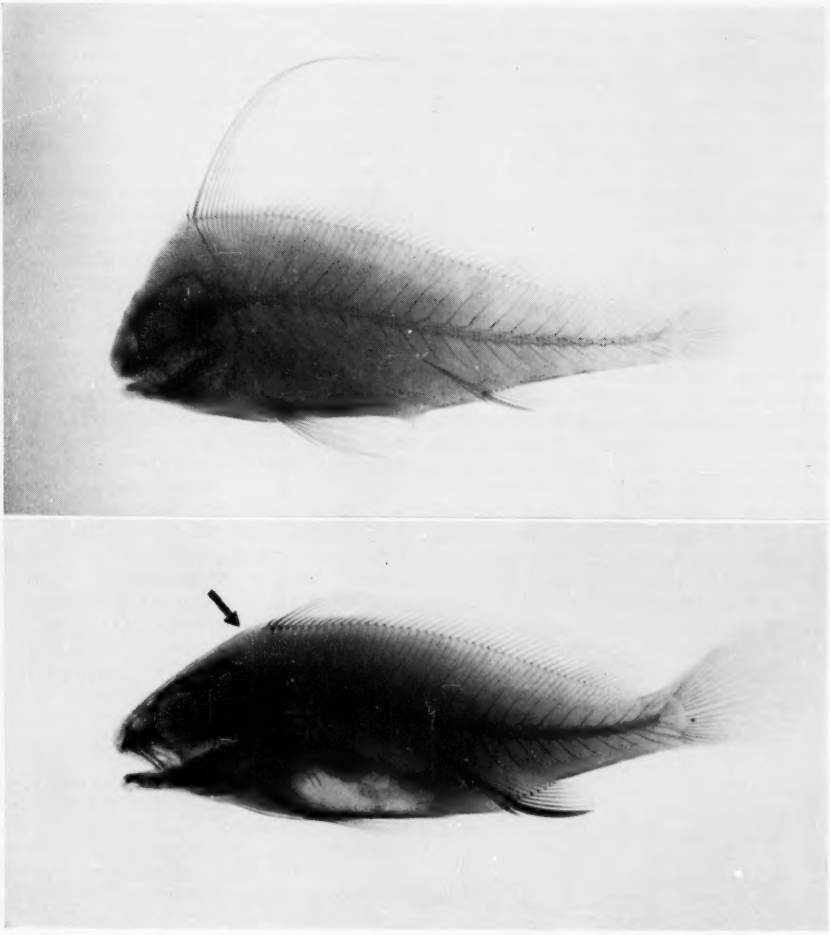

Fig. 1. Radiographs illustrating the skeletal differences between *Equetus* and *Pareques*. Top figure *Equetus lanceolatus* UF 7870, bottom figure *Pareques viola* BC57-140. The arrow in the bottom figure indicates the position of the free interneurals.

Pareques viola (Gilbert)

Eques viola Gilbert, in Jordan and Evermann 1898:1486, Panama Bay. Gilbert and Starks 1904:138, pl. 21, fig. 42, Panama Bay.

Description.—Head 2.5 to 4.2 in total length; depth 3.3 to 3.8 in total length. D. VIII to XI or X–I, 38 to 46; A. II, 6 to 8. Scales in 54 to 68 transverse rows below lateral line. Greatest body depth at origin of soft dorsal, after which the back tapers smoothly down to the caudal peduncle. Caudal peduncle 2.5 to 3.7 in head. Snout 3.4 to 4.5 in head. Eye 3.5 to 5.0 in head. Gillrakers short, 5 to 7 + 11 to 15. Pyloric caeca 6 to 8. Soft dorsal and anal densely sheathed in scales; pectorals and ventrals with series of scales on the membranes. Second dorsal spine longest, 1.6 to 2 in head. Second anal spine enlarged, 1.9 to 2.8 in head; anal rays extend well beyond second anal spine. Pectorals inserted slightly in front of ventrals, pectorals and ventrals almost of equal length; pectoral 1.2 to 1.6 in head. Axillary scales of ventrals poorly developed.

Coloration.—*Pareques viola* has two distinct color patterns: a solid dark color, and a

light color with 6 to 9 dark horizontal stripes. A comparison of the striped and unstriped forms of *P. viola* revealed no significant differences other than coloration. A collection from Cape San Lucas (BC57-140) contained both striped and unstriped specimens as well as some individuals with an intermediate color pattern. The same variation in color pattern occurs in the Atlantic species *Pareques acuminatus*. Springer and Woodburn (1960:54) attribute the variation in the color pattern of *P. acuminatus* to differences in age. Small specimens are said to have dark stripes over a light background, while larger specimens are a solid dark color. This is not the case in *P. viola*. In the specimens examined the striped form ranged from 60 to 200 mm. in length, and the unstriped form from 90 to 220 mm. Both color patterns were found in juvenile and mature specimens, and in males and females.

There is no consistent pattern in the geographical distribution of the color forms of *P. viola*. Both color forms occur in the Gulf of California, although the dark form predominates. The striped form is the most common in the Revillagigedo and Tres Marias Islands. Specimens from Panama Bay are all unstriped, and a single specimen from Cabo Blanco, Peru is striped. As a generalization, the insular populations examined tended to be predominately striped and mainland populations predominately unstriped. This suggests that the variation in color pattern is due to ecological factors.

Range.—From Point Eugenio on the west coast of Baja California, and the entire Gulf of California to Cabo Blanco, northern Peru.

Material examined.—W50-206(1) Point Peñasco; W51-11(8) San Guillermo; W51-62(12) Point Guillermo; W52-41(6) Port San Carlos; W55-282(1) 2 or 3 miles N. of San Carlos Bay; W55-243(1) West of Los Tetas de Cabra, Sonora, Mexico. H53-178(2) Los Angeles Bay; W51-221(3) Cape Eugenio; W55-85(1), W55-93(1) Magdalena Bay; W52-259(2) San Lucas Bay; BC57-140(11) Cape San Lucas, Baja California, Mexico. BC59-241(1) Maria Magdalena Island, Tres Marias Islands, Mexico. BC54-58(1), BC57-149(5), BC57-155(2), BC57-158(1), SIO58-148(1), W55-125(1), Socorro Island, Revillagigedo Islands, Mexico. CNHM 21664, 21665, 21666(3), USNM 80740(3), USNM 167139(3), Panama Bay, Panama. BC56-159(1) Cabo Blanco, Peru.

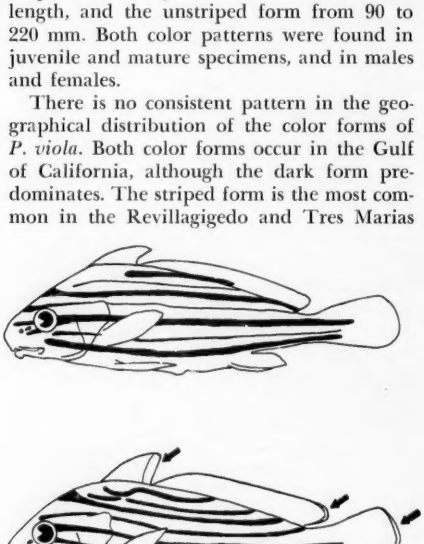

Fig. 2. Color patterns of eastern Pacific species of *Pareques*. Top figure is striped form of *Pareques viola*, center figure is *Pareques fuscovittatus*. The arrows indicate white fin margins; bottom figure is *Pareques lanfeari*.

Pareques fuscovittatus (Kendall and Radcliffe)
Eques fuscovittatus Kendall and Radcliffe 1912:125–6, Acapulco, Mexico.

Description.—Head 3.6 to 4.0 in total length; depth 3.5 to 3.7 in total length. D. IX to XI, 39 to 42; A. II, 7. Scales in 55 to 65 transverse rows below lateral line. Greatest body depth at origin of soft dorsal, after which the back tapers smoothly down to the caudal peduncle. Caudal peduncle 3.2 to 3.4 in head. Snout 3.4 to 3.6 in head. Eye 3.8 to 4.3 in head. Gillrakers short, 5 to 7 + 11 to 14. Pyloric caeca about 6. Soft dorsal and anal densely sheathed in scales; pectorals and ventrals partially sheathed in scales. Second dorsal spine longest, 1.5 to 2 in head. Second anal spine enlarged, 2.5 to 2.8 in head. Pectorals inserted directly under ventrals, pectorals and ventrals almost of equal length, pectorals 1.4 to 1.6 in head. Axillary scales of ventrals poorly developed.

Coloration.—Six to seven horizontal dark stripes on body, the four ventral stripes extending onto the head. The first dorsal stripe is curved abruptly downward below the spinous dorsal. The spinous dorsal has a wide white margin at the posterior edge. The soft

dorsal and caudal have a narrow white margin.

Relationship Between *P. fuscovittatus* and *P. viola*

Morphologically *P. fuscovittatus* is very similar to *P. viola*; the only detectable difference is in the color pattern. All of the specimens examined that are referred to *P. fuscovittatus* are characterized by a distinct wide white margin on the posterior edge of the spinous dorsal, and an abrupt downward curve in the first dorsal stripe. None of the striped specimens identified as *P. viola* show this character (Fig. 2). No intermediate individuals were observed. For this reason *P. fuscovittatus* is retained as a distinct species, although further investigation may show that it is another color form of *P. viola*.

Range.—From Chacala, Nayarit to Acapulco, Guerrero, Mexico.

Material examined.—BC57-116(2) Chamela Bay; W56-234(4) Manzanillo, Colima, Mexico. W58-5(1) Chacala, Nayarit, Mexico.

Pareques lanfeari (Barton)

Eques lanfeari Barton 1947:1–3, Talara, Peru.

Equetus lanfeari Hildebrand and Barton 1949:17–21, Talara, Peru.

Description.—Head 3.5 to 3.7 in total length, depth 3.4 to 3.7 in total length. [Only one specimen of *P. lanfeari* was examined. The ranges in counts and body proportions are derived from Hildebrand and Barton (1949).] D. IX–I to XII, 35 to 37; A. II, 7 to 8. Scales in about 60 transverse rows below the lateral line. Greatest body depth at center of spinous dorsal, after which the back tapers smoothly down to the caudal peduncle. Caudal peduncle 3.4 to 3.6 in head. Snout 3 to 4.2 in head. Eye 4.4 to 4.7 in head. Lower jaw without a prominent symphyseal knob. Gillrakers short, 6 + 12. Pyloric caeca 7. Soft dorsal and anal sheathed in scales for about two-thirds their height. Second dorsal spine the longest, 1.6 to 2.2 in head. Second anal spine enlarged, 2 to 2.2 in head; anal rays extend well beyond second anal spine. Pectorals inserted slightly in front of the ventrals, pectorals and ventrals almost of equal length, pectorals 1.5 to 1.6 in head. Axillary scales of the ventrals poorly developed.

Coloration.—Four distinct, dark horizontal stripes on the body. These stripes do not extend onto the head (Fig. 2).

Range.—Talara to Chimbote, Peru.

Material examined.—BC56-171(1) Lobos de Tierra Island, Peru.

Specific relationships.—Morphologically *Pareques* is somewhat intermediate between *Equetus* and the more generalized genus *Sciaena*, as indicated earlier. The heavily ossified interneurals anterior to the first dorsal fin, and the low number of dorsal rays suggest that *P. lanfeari* is close to *Sciaena*, and therefore is probably the most primitive of the known species of *Pareques*. *P. viola* and *P. acuminatus* are very similar morphologically and represent geminate species. They probably evolved from a single ancestral form separated in the late Pliocene or early Pleistocene by the present Panamanian landbridge. *P. fuscovittatus* is also closely related to *P. viola* and probably diverged quite recently. Fig. 3 represents a possible phylogeny of *Pareques*.

Some speculations can be made on the origin of *Equetus* and *Pareques*. All of the species of *Equetus* are confined to the tropical western Atlantic. Three of the species of *Pareques* are restricted to the tropical eastern Pacific, and one species is found in the tropical western Atlantic. Morphologically, *Pareques* is more primitive, and is probably ancestral to *Equetus*. *Pareques* probably originated in the tropical eastern Pacific and from there spread into the Atlantic. In the tropical western Atlantic this primitive form of *Pareques* could have given rise to *Equetus*.

Acknowledgments.—Dr. J. C. Briggs di-

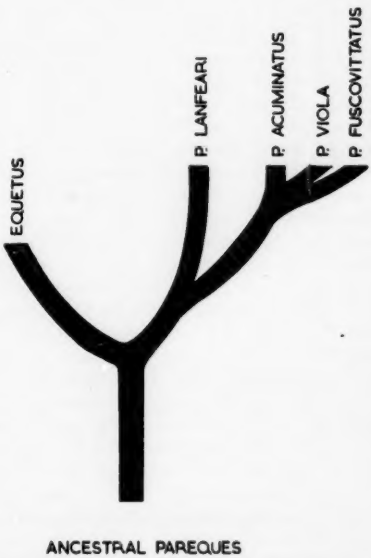

Fig. 3. A suggested phylogeny of *Pareques*

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Institute of Fisheries, The University of British Columbia, Vancouver, Canada.

Salinity Tolerances of Some Fishes of a Southern California Coastal Lagoon[1]

Lars H. Carpelan

During the course of an ecological study of certain coastal lagoons in San Diego County, California, one lagoon proved to be of interest to the problem of salt tolerance because it was open to the ocean during the first half of a year of study but was closed by a sand bar during the second half of the year. The marine fish trapped by the closing of the bar were subjected to several obvious changes in their environment, the most conspicuous of which was an increase in salinity from 35 0/00 to 60 0/00. The limit of tolerance of various species of fish to the changed conditions was evidently exceeded because one species after another was eliminated. It is, of course, impossible to say that this was due to salinity alone because other factors, such as temperature, pH, concentration of dissolved oxygen and food availability were changing simultaneously.

Day (1951) has commented that rather than any single factor, it is probably the action of various factors in combination that acts to limit the distribution of organisms. However, as pointed out by Pearse and Gunter (1957) it is difficult to differentiate all the factors that determine the presence of organisms within a salinity range, and salinity is, definitely, one limiting factor. The problem of salt tolerance has the allied problem of osmoregulation, which is adaptation to changes in salinity. The general problem of osmotic regulation in fishes was discussed by Keys (1933); the physiology of osmoregulation in fishes has been summarized by Black (1951). Pearse and Gunter (1957) have more recently reviewed osmoregulation in vertebrates, including fishes. However, although the problem and the salt tolerance of some species of fishes has been studied, e.g., *Fundulus* by Keys (1931), *Chanos* by Pannikaar (1951), the tolerance of most species in nature is not known. Simmons (1957) has listed the salinity tolerances of fishes observed in the Laguna Madre, Texas. Hedgpeth (1959) has compiled

[1] Supported by an agreement (WC–103) between the State of California Department of Fish and Game and the University of California.

a list of the metazoa, including fishes, reported to have occurred in salinities greater than 45 0/00. Hedgpeth (1957) offered a preliminary tabulation of the upper salinity tolerances of organisms, which included fishes as having an upper tolerance of 75–85 0/00. But, according to Hedgpeth, "... it is difficult to assemble a list of organisms according to their known salinity tolerances ..." because "... often no salinity data are given in the references to the occurrence of organisms in high salinities ...." Furthermore, there is also lack of information regarding other variables in the environment, as commented on by Day (1951), which alone or together with salinity might limit the distribution of organisms.

The observations made during the study of Los Penasquitos lagoon allow inclusion of data, presented in Part I, which show some, at least, of the environmental factors of concern. In Part II is presented a discussion of the possible upper limit of salt tolerance, under the particular conditions present, of species of fish observed in the lagoon, as well as observations regarding the prevalence and size of fish taken during the study.

Environmental Factors

Description.—Los Penasquitos lagoon is located about three miles south of Del Mar, California, and just north of the Torrey Pines State Park. Although it lies in a wide valley, the lagoon was limited, during the period of study, to a narrow channel paralleling the road to the Carmel Valley. Routine collections were made at three stations. Station A, about 0.1 mile from the ocean, was essentially the seaward end of the lagoon. The depth of water at Station A was about five feet; between it and the ocean the water at low tide was only a few inches deep during the period when the lagoon was open to the ocean, and when it was closed, the sand bar that formed extended inland to Station A. Station B, about a half-mile inland from the shore, was located in the widest portion of the lagoon (about 100 feet) which was also the area of deepest water (about 27 feet). Station C was the upper limit of water with a depth of more than one or two feet. It was located about a mile from the ocean.

Rainfall.—At Del Mar (three miles north of Los Penasquitos) the rainfall, as recorded by the Southern California Gas and Electric Company, totalled 19.9 inches for the rainfall year 1957–1958, compared to an average of 10.66 inches per year during the five previous years. Since most of the rain had fallen during February, March and April, 1958, (see Fig. 1), even the upper end of the lagoon (Station C) showed little dilution at the start of the study (which began in June, 1958); the salinity was 33–34 0/00 in June and July, 1958. In contrast to the above-normal rainfall during 1957–1958, the rainfall year 1958–1959 (July, 1958 to June, 1959) was a year of less than average rainfall. At Del Mar only 5.92 inches fell during 1958–1959; most of the year's rain (3.65 inches) came during February. The small amount of rain that fell in April had no noticeable effect on the salinity increase that began in March and continued until the end of the study in September.

Temperature.—The surface temperatures at the shallow uppermost station were about the same (25°–30° C.) during the summer of 1959, when the lagoon was closed, as they had been during the summer of 1958, when the lagoon had been open to the ocean. On the other hand, at Station A, the location nearest the ocean and subjected to greater tidal effects, summer temperatures from June to October, 1958 were in the range from 20° to 25° C. (which was about 5° C. lower than at Station C); but in the summer of 1959 the surface water temperatures tended to be the same at all stations in the range from 25° to 29° C. In other words, the fish trapped in the lagoon by the closing of the bar were subjected to water temperatures 4°–5° C. higher during the summer of 1959 than during the same period in 1958. The higher temperature range and the increase in temperature may be considered, in conjunction with the increase in salinity, as a factor limiting marine fish from the lagoon. Subsurface temperatures were taken only at station B, where as late in the year as May, 1959 there was a big gradient in temperature from surface to bottom; on May 23 the surface temperature was 24.5° C., and the bottom temperature was 17.5° C.

A month later, on June 23, the difference was only 1.5° C.: 24.5° at the surface, 23° at the bottom. In July, August and September there were differences of only 1° between surface and bottom temperatures. Therefore, during the critical period for most of the fish, which seemed to have been during June and July, 1959, there was no colder water to which the fish could escape. Thus, during the period while the salinity increased from 33 0/00 to 60 0/00, water temperature increased

from 17° C. (March, 7) to 28° C. (June, 23) and remained between 25° and 29° during July, August and September at all locations within the lagoon.

Salinity.—At the maximum salinity present in September (60 0/00) there was no perceptible precipitation of any ion, and with the exception of an apparently slight increase in proportion of carbonate ion (see hydrogen ion concentration, below) the proportion of ions remained the same throughout the period of study. That is, although the organisms living in the lagoon were subjected to increased concentration of all ions, they were probably not subjected to any great change in proportion of ions.

Routine determinations of salt concentration in the lagoon were made by titration of halides with silver nitrate in the presence of chromate indicator (Mohr method; p. 60 of *Standard Methods, 10th ed.*, 1955). Specific conductance, determined with a conductivity bridge, was used as measure of total ions present, and as a check on the chlorinity determinations.

Fig. 2a shows that the salinity at both the lower (Station A) and the upper (Station C) parts of the lagoon was approximately that of coastal sea water during the last half of 1958. After the closing of the bar in early January, an increase in salinity which began in January was checked by dilution due to rainfall and run-off in February and early March. From March until September, 1959 there was a steady increase in salinity: from 35 0/00 on March 7, salinity increased to 60 0/00 on September 3, which was an almost linear increase at the rate of a little over 4 0/00 per month.

Fig. 2b shows that although the surface salinity at Station B was about the same as at the other two stations, the salinity at depths below 20 feet ranged from 38 0/00 to 43 0/00 during August, September and October, 1958 compared to surface salinities of 34 0/00 to 35 0/00. From March through September, 1959 (the period of concern) the salinity was the same at surface and bottom.

Hydrogen Ion Concentration.—Table 1 shows the pH values taken in the field with a Beckman Model G portable pH meter. Los Penasquitos lagoon was subject to great

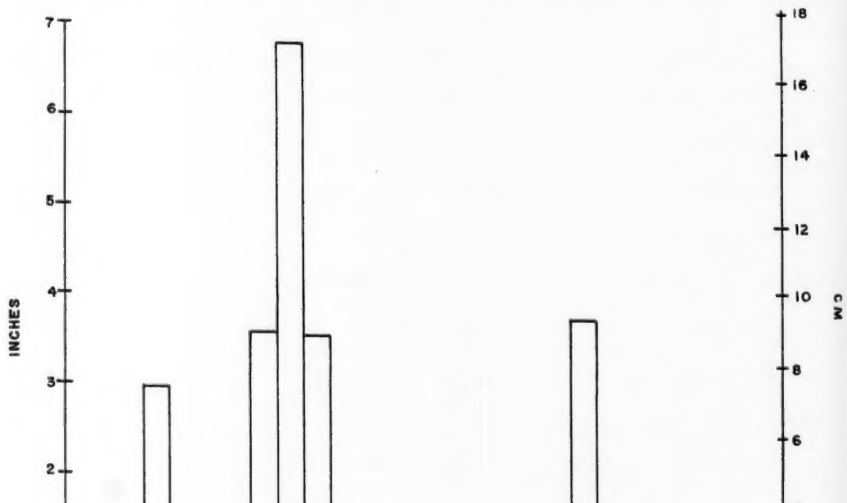

Fig. 1. Rainfall, Del Mar, California.

variation in pH. Surface values ranged from 6.4 to 9.0 both before and after the closing of the bar. Although the pH was generally higher during the summer of 1959 (coincident with the time of greatest salinity) than it was during the summer of 1958, it was not higher than it had been on occasion during the period when salinity was comparable to that of coastal sea water.

Dissolved Oxygen.—Dissolved oxygen was determined by the unmodified Winkler method (*Standard Methods, p. 252, 10th ed.,* 1955).

Fig. 3 indicates that the concentrations of dissolved oxygen at the surface were adequate to support fishes, but that there were diurnal and annual fluctuations, and periods of bottom anoxia. Although periods of oxygen depletion after the lagoon was closed were not more pronounced than they had been while the lagoon was open to the ocean, the generally lowered concentration of oxygen, due to decrease in solubility with increase in salinity, may, in conjunction with the increased osmotic effects, have been a factor of concern in the elimination of organisms from the lagoon.

The Fishes of Los Penasquitos Lagoon

Some of the fishes recorded below as present in Los Penasquitos are represented by a single collection, others were taken frequently and in large numbers, so the data are very uneven and incomplete. Where data are sufficient to permit, size groups are given, and where possible, limits of salt tolerance are estimated for the species enumerated below.

Fundulus parvipinnis Girard. Twelve specimens were taken by seine on three occasions in July and August, 1958. One collection of nine killfish taken on July 30, representative of the size present, included eight individuals having an average length of 7.9 cm. (range from 7.4 to 8.7) and an average weight of 8.3 grams (range from 7.7 to 12.1), and one smaller specimen 4 cm. long which weighed 0.9 grams.

On June 23, 1959, (the salinity on that date was 51 0/00) a total of 15 specimens were

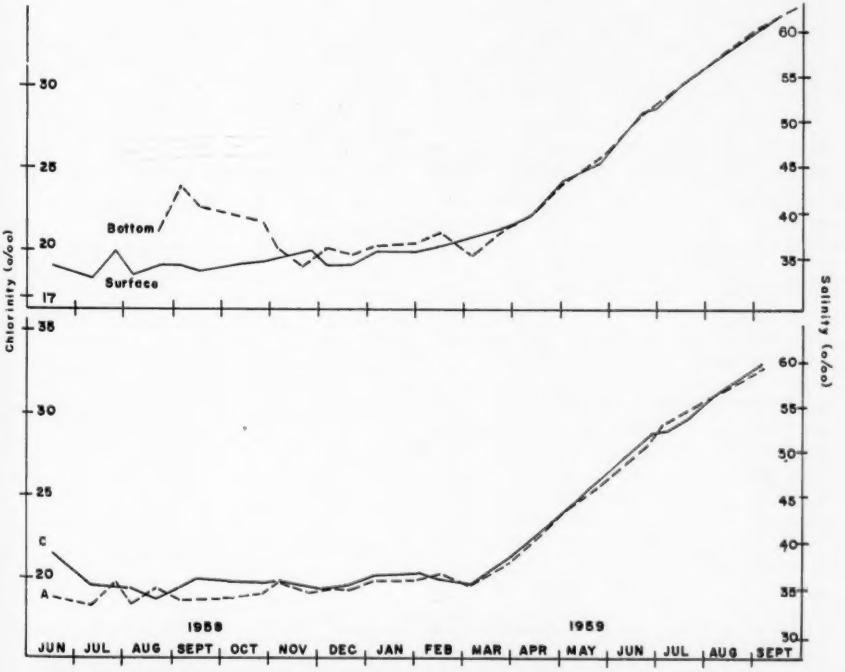

Fig. 2a. (lower) Surface salinity, stations A and C, Los Penasquitos Lagoon, California.
Fig. 2b. (upper) Surface and bottom salinity, station B, Los Penasquitos Lagoon, California.

TABLE 1. pH VALUES, LOS PENASQUITOS LAGOON, 1958–1959

Date	Station A (Surface)	Station B (Surface)	Station B (Bottom)	Station C (Surface)
June 18	7.6	8.3	—	9.0
July 9	7.8	6.4	7.6	8.4
July 23	8.2	8.0	8.1	7.9
Aug. 6	8.1	7.7	7.4	7.8
Aug. 20	8.15	7.9	7.5	7.8
Sep. 4	7.9	8.0	—	7.8
Oct. 11	7.9	7.1	—	7.8
Oct. 25	7.45	8.1	7.25	8.0
Nov. 8	6.4	6.5	6.4	7.3
Nov. 22	7.65	7.9	—	7.7
Dec. 6	7.8	7.8	8.15	8.1
Dec. 20	7.8	7.9	7.9	7.9
Jan. 3	5.9	7.2	6.0	6.6
Jan. 31	7.25	7.15	7.2	7.3
Feb. 14	(Meter inoperative)			
Mar. 7	7.3	7.5	—	7.25
Mar. 28	6.5	7.15	—	6.55
Apr. 12	7.65	7.0	—	7.5
May 2	7.2	7.5	8.0	7.2
May 23	7.2	7.7	8.0	7.1
June 23	(Meter inoperative)			
July 1	8.2	8.0	8.0	8.3
Aug. 6	8.2	8.3	8.15	8.2
Sep. 3	8.55	8.7	8.4	8.8

taken by poisoning with rotenone (Pro-Noxfish) at three stations. The average length was 6.2 cm. (range from 5.0 to 7.2) and the average weight was 3.6 grams (range from 2.8 to 6.5). On July 1, 1959, 13 specimens of *Fundulus* were taken, also by poison, at Station C. On August 6, 1959, a single *Fundulus*, taken by poison at Station A, was the last specimen taken from Los Penasquitos. The salinity on August 6 was 55 0/00. Since the next collection, on September 3, 1959, was only by gillnet, the maximum tolerance of *Fundulus* was not observed.

Paralichthys californicus (Ayres). Only small specimens, ranging from 5 to 7 cm. in length, were taken (by seine) during 1958. On June 23, 1959, although the salinity had increased to 51 0/00, *Paralichthys* was, apparently, still numerous because five specimens were present in a gillnet collection. They seemed to represent three size classes:

Class	Average length	Average weight
1	10.3 cm.	16 gm.
2	18.5	90
3	29.3	373

On July 1, although the salinity had increased only slightly—to 53 0/000—only one specimen (24.3 cm. in length weighing 91 grams) was taken by gillnet At the next monthly sampling (August, 6) none were taken, and some were seen dead on shore. The salinity on August 6th was 55 0/00. It would thus seem that the maximum salinity

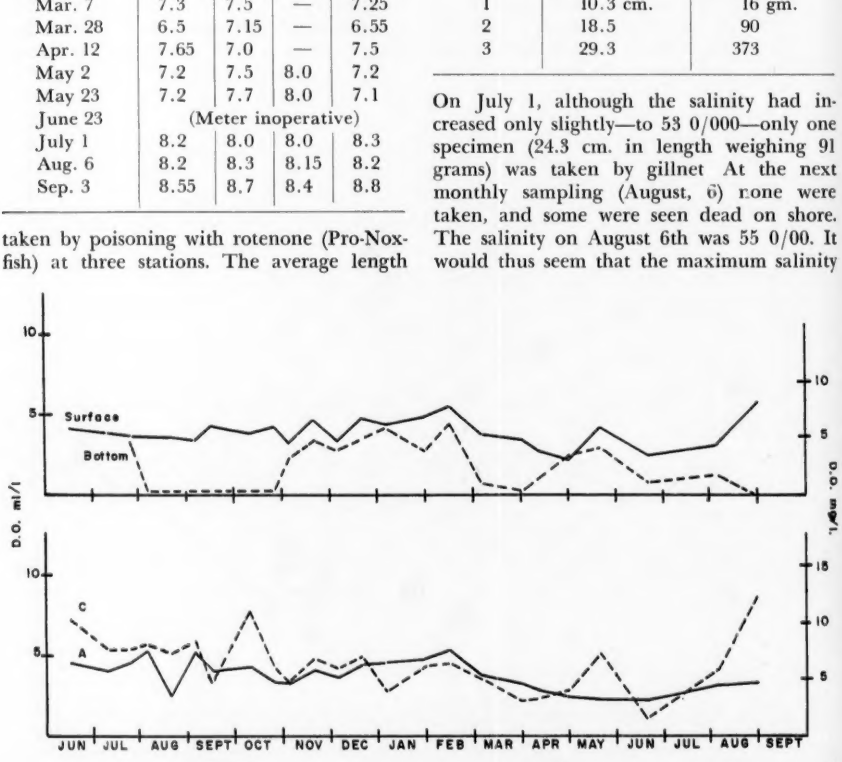

Fig. 3a (lower) Dissolved oxygen, stations A and C, Los Penasquitos Lagoon, California.
Fig. 3b (upper) Dissolved oxygen, surface and bottom, station B, Los Penasquitos Lagoon, California.

tolerated by *Paralichthys* is between 50–55 0/00.

Hypsopsetta guttulata (Girard). Small specimens of the turbot, 7 to 10 cm. long, were taken by seine during 1958 while the lagoon was open to the sea. Gillnet collections on June 23, 1959, included 17 specimens 10 to 16 cm. in length and 21 to 89 grams in weight. On the same date six specimens of the same size range were taken by poison. On July 1 and on August 6, 1959, *Hypsopsetta* was still present in number—13 were taken by gillnet on August 6. They were in the same size range as the specimens of the June collection. On September 3, 1959, only one specimen (11.4 cm. long, 34.1 gm. in weight) was taken by gillnet. Since the shore was lined with dead and dying turbots, the maximum salt tolerance of this species seems to be about 60 0/00 which was the salinity on September 3.

Syngnathus sp. Specimens taken by seine in 1958, when the lagoon was open to the sea, ranged in length from 7 to 20 cm. and in weight from 1 to 2.3 grams. On June 23, 1959, a total of six specimens was taken by poison at three stations. They ranged from 15 to 27 cm. in length and from 1.2 to 7.5 grams in weight. Although similar poisoning operations were made on July 1 and on August 6, the June 23 specimens were the last ones seen or taken. The salinity on June 23, which was 51 0/00, may thus be about the upper limit of salt tolerance of the pipefish.

Atherinops affinis littoralis Ayres is the most prevalent fish in Los Penasquitos and, apparently, also the most salt-tolerant. The first collection, of 81 specimens, was taken by seine on July 30, 1958. They were all judged to be young of the year, averaging 3.2 cm. in length and 0.29 gm. in weight (range 2.3 to 3.9 cm., 0.11 to 0.45 gm.). A sample of 35 specimens obtained by seine on August 6, 1958, could be divided into the following three size groups:

Size Group	Length		Weight	
	Average cm.	Range. cm.	Average gm.	Range gm.
1	3.6	3.2–4.0	0.37	0.23–0.47
2	5.1	4.7–5.6	1.27	1.0 –1.7
3	7.8	7.4–8.3	4.95	3.75–6.65
Total	4.9	3.2–8.3	1.8	0.23–6.65

All the fish included in the tabulation above probably belonged to the same age group, having been spawned at different times during spring and summer of 1958. However, the largest class could conceivably have been spawned in late summer or fall of 1957. By the 20th of August, 1958 the smallest size class, in 75 specimens taken by seine, averaged 4 cm. in length and 0.6 gm. in weight; the two larger classes maintained about the same size and weight as indicated in the tabulation for August 6th.

On June 23, 1959, which was nearly seven months after the lagoon had been closed off from the ocean, among 138 specimens of *Atherinops* taken by rotenone at three stations, the smallest group averaged 4 cm. in length and 0.6 gm. in weight. Two larger groups could be differentiated: one averaged 10.2 cm. in length and 12.8 gm. in weight; the other averaged 15.3 cm. and 41.3 gms. in length and weight, respectively.

On August 6, 1959, 60 specimens, taken by both gillnet and by poison, fell into four size groups:

Average length	Average weight
5.5 cm.	1.9 gm.
10.4	13.3
12.9	24.2
15.6	42.3

There seemed to be in August, 1959 an absence of *Atherinops* of the smallest size that had been present in August 1958 (that is, there were no fish with a length of 4 cm. and a weight of less than one gram). The most logical but not the only explanation for the absence of small fish would seem to be that the increasing salinity either had shortened the spawning period in 1959, limiting it to the period prior to May, or that fish hatched later than May had not lived until August. The smallest fish taken in August (the group averaging 5.5 cm. in length) could well have been hatched four months previously (in May) when the salinity was 45 0/00. It has been observed elsewhere (Carpelan, 1955) that although another subspecies of *Atherinops affinis* spawned at salinities beyond what was present in Los Penasquitos, the young lived for only about four months, succumbing when about 3 cm. in length. It may, therefore, be that it was not the shortening of the spawning period (by increased salinity) but the death of the young after hatching that led to the absence of small *Atherinops* from the August collections.

On September 3, 1959, 42 of 45 specimens of *Atherinops* in gillnet collections had an average length of 12.3 cm. and an average weight of 23.3 grams. Three specimens of a larger size were also present; they averaged 15.2 cm. in length and 47 grams in weight. The salinity on September 3 was 60 0/00. Neither then nor on October 2, 1959, when the salinity had reached 63 0/00 was there any evidence of distress, so the upper limit of salt tolerance of larger adult *Atherinops* is beyond 63 0/00.

Paralabrax clathratus (Girard). Two specimens were taken by gillnet on June 23, 1959. None were taken subsequently either by gillnet or poison, so the salinity of about 51 0/00, which was the salinity of June 23rd, may be near the upper limit of salt tolerance of this species.

Girella nigricans (Ayres). Three small specimens of the opaleye were present in each of two seine collections made on August 6, 1958. At Station A the average length was 3.0 cm. (range 2.8 to 3.2) and the average weight was 0.47 gm. (range 0.36 to 0.56). At Station B the average length of the three specimens was 5.3 cm. (range 4.8 to 5.6) and the average weight was 4.15 gm. (range from 3.0 to 5.1 gm.). On June 23, 1959, two specimens were taken by poison at Station A. Larger than the specimens obtained in 1958, the lengths were 6.9 and 7.9 cm. and the weights were 8.6 and 13.5 grams. Two other specimens, taken with poison on August 6, 1959, were the last ones collected. They were 9.5 cm. and 11 cm. in length, and weighed 25.5 and 43 gms. Since neither poison nor seine collections were made subsequent to August 6, it was not learned how much greater salinity *Girella* is able to withstand than the 55 0/00 present on August 6.

Menticirrhus undulatus Girard. One specimen 19 cm. long and weighing 74 grams was among the fish collected by gillnet on June 23, 1959. This was the only specimen ever observed in Los Penasquitos. It was evidently able to tolerate the salinity of 51 0/00 which was then present.

Leptocottus armatus Girard. Two specimens were taken by seine on July 30, 1958. Their sizes ranged from 5.2 to 8.9 cm. in length and from 1.3 to 8.4 gms. in weight. Eight specimens were taken by gillnet on June 23, 1959. Their average length was 11.6 cm. (range from 9.5 to 16.4) and their average weight was 32.3 gms. in the range from 18.1 to 80 grams. One other specimen, taken on June 23 by rotenone was 12.3 cm. long and weighed 34 grams. No specimens were taken subsequent to June 23, although both rotenone and gillnet collections were made on July 1 and on August 6. So it seems likely that the upper limit of salt tolerance of *Leptocottus* is in the vicinity of 51 to 53 0/00, which was the salinity of Los Penasquitos at the end of June, 1959.

Cymatogaster aggregata Gibbons. A collection of four specimens, taken by seine on August 6, 1958, was the only collection of shiner perch made in Los Penasquitos. The average length was 6 cm., the average weight 5 grams.

Eucyclogobius newberryi (Girard). This goby was collected only on June 23, 1959, when it was taken by rotenone at both Stations B and C. The 13 specimens collected at Station C seemed to fall into four size classes.

Class	Average length	Average weight	Number in Class
4	12.8 cm.	37.2 gm.	1
3	9.5	13.8	2
2	5.8	3.0	6
1	3.7	0.7	4

Five specimens collected at Station B had an average length of 5.8 cm. (range from 5.3 to 6.2) and an average weight of 2.85 grams (range from 2.2 to 3.6 gms.). Thus only one size class seemed to be represented at Station B. Since the goby was not taken by similar poisoning operations on July 1 and on August 6, there is presumptive evidence that it had about reached its limit of salt tolerance at the end of June when the salinity reached 53 0/00.

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Summary

A coastal lagoon, which was open to the ocean during the first six months of a period of observation and sampling, was closed off during the following eight months of study. Salinity increased from 35 0/00 to over 60 0/00. Compared to conditions present while the lagoon was open to the ocean, after the

closing of the bar summer water temperatures were 4–5° C. higher, the pH was generally 0.6 to 1.0 pH unit higher, and the concentrations of dissolved oxygen were slightly lower. However, since both pH and dissolved oxygen had been as variable prior to closing of the lagoon as afterward, the main physical factors of concern were temperature and salinity, of which the latter showed the greater change.

Of 10 species of fish trapped in the lagoon when it closed, the majority tolerated the changing conditions until the salinity reached 50–55 0/00. *Hypsopsetta guttulata* withstood the conditions a little longer—until the salinity was 55–60 0/00. No upper limit of tolerance was observed for *Fundulus parvipinnis* and *Girella nigricans*, nor for *Atherinops affinis littoralis*, some which were still thriving, at a salinity of 63 0/00, when the study terminated.

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Department of Biology, University of California, Riverside.

Lateral Lines and an Undescribed Sensory Area on the Head of the Gulf Menhaden, *Brevoortia patronus*

Gordon Gunter and William J. Demoran

THE founders of ichthyology noted that most fishes had lateral lines along the body. Later it was found that the lateral line system was present on the head.

We have not attempted to trace the origin or sequential development of knowledge of the cephalic lateral lines. However, Günther (1880:49) stated that the "muciferous duct" of the lateral line is continued on the head and he mentioned the main branches, which were later delineated in the generalized figure by Goodrich (1930). Bridge (1904) discussed the cephalic lines of cyclostomes, elasmobranchs and teleosts and Berg (1947:419) indicated that they are typical of teleosts.

Cephalic lateral lines are probably present in all fishes, although the body lines are absent in many species. In descriptive ichthyology by far the greater emphasis has been placed upon the body lateral lines because the scale counts are related to them. Furthermore, the cephalic lines are often inconspicuous, being imbedded in the integument or the bones, and in many fishes they have gone unnoticed and remain to be described. For instance, Gunter (1936) first mentioned the accessory and cephalic lines of the Achiridae, Wohlfahrt (1937) described the cephalic lines of *Clupea pilchardus* and Bramford (1941) described the cephalic lines of the common herring, *Clupea harengus.*

The cephalic lines have been used in taxonomic studies of some fishes, such as the North American Cyprinidae. Illick (1956) made a general study of this group. She found that she could separate all genera, but not quite all species, on the basis of the cephalic

Fig. 1. A photograph of the head of *Brevoortia patronus* Goode brushed with india ink to show the cephalic lateral lines. ×1½.

lines. Her paper cites much of the important literature.

According to Wohlfahrt, the cephalic canals of *Clupea pilchardus* do not lie in the bone of the "dermatocranium." They are all developed in the subepidermal layer of the corium. Bramford stated that in *Clupea harengus* the canals lie "remarkably free from the bones." The case is the same in *Brevoortia*. Nevertheless, the development of the cephalic canals is somehow related to the morphogenesis of the dermal bones of the skull, for they are characteristically found on certain bones and not on others. Thus, it is customary to say that the lines are found on or covering certain bones.

The pattern of the cephalic lateral lines of the clupeoid fishes is somewhat different from those of other teleosts, as described by Bridge (*op. cit.*) and by Goodrich. Berg (1947:420), in speaking of the superfamily Clupeoidae, says that in some genera ramifications of the sensory canal "spread on the opercular and subopercular—a feature unique among the living Actinopterygii." He mentioned the genera *Alosa, Caspialosa, Clupeonella, Sardina* and *Engraulis*. According to Wohlfahrt (*op. cit.*) the line organs of the head lie on all bones of the dermatocranium of *Clupea pilchardus* except the premaxillary, maxillary and interoperculum.

Cephalic Lines on the Gulf Menhaden

Cephalic lateral lines on the common Gulf menhaden, *Brevoortia patronus*, were noted while meristic counts were being made on frozen fish in connection with racial studies. The canal system was not noticed until the fish were brushed lightly with india ink to make the scales stand out. Fig. 1 is a photograph of an inked fish showing the cephalic sensory canals. Fig. 2 shows more detail of the same photograph.

The main canal comes to the surface back of the eye under the adipose eyelid, with four arborescent branches leading out to the opercle and preopercle. A main trunk runs under

the eye, with many smaller branches, and forward of the eye onto the snout even with the nostril. Smaller branches run forward above the eye to a little beyond the pupil. Two large branches on the dorsal part of the opercle do not connect on the surface with the large branch back of the eye.

Fig. 1 shows that branches of the cephalic lines are present on the pterygoid, quadrate, preoperculum and operculum. There is a branch on the mandible that does not show clearly in the photograph. The lines are not present on the premaxillary, maxillary and interoperculum (similar to *Clupea*), and are also absent from the suboperculum. *Brevoortia* has the lines on the operculum and thus belongs with the group of clupeoids which Berg referred to as unique among the Actinopterygii, although the lines are absent from the suboperculum.

A branch of the lateral line runs above and back of the operculum, ending on the unscaled post-opercular margin of the body in a sickle-shaped area, with some endings running out onto the first two or three body scales. Thus, part of the endings are actually within the gill chamber and would be of little use when the gill cover is closed. With regard to the Clupeidae, Berg (*op. cit.*) stated that the lateral line traverses "only the anterior 2–5 scales." Actually, that part of the system, as well as the part on the unscaled trunk margin of the gill chamber, consists of fine endings of a large canal from the head.

Certain small configurations on the naked, spongy area above and posterior to the eye show up with inking, suggesting that some pores come to the surface on this area without connecting branches on the surface. The connection of the pores on top of the head with the cephalic lateral line system is shown by the fact that, with the use of an aquarium aerator as a pump, india ink can be pumped into the whole cephalic line system. This means essentially that this spongy region is functionally a part of the cephalic line system, and so far as we know this fact has never been recorded. It is a triangular region above and posterior to each eye connected by an isthmus across the head just forward of the nape region. The naming of this part of the lateral line complex is beset with some difficulty. The name lateral line itself is an areal name, non-committal as to function. The term cephalic lateral line is something of a misnomer, but it implies the essential similarity of function of the body and cephalic

Fig. 2. Detail of a part of the operculum of *Brevoortia patronus* in Fig. 1. ×2.

lines. We propose to follow the custom with regard to lateral lines and name the region the cephalic spongy sensory area. It probably exists in a large number of other clupeoids. We venture to suggest that injection of a local anaesthetic or narcotic into the cephalic line system through the spongy sensory area might permit experimental studies of the lateral line complex without the necessity for cutting the internal nerves.

According to Wohlfahrt the principal canal of the head of *C. pilchardus* lines in the "Recessus lateralis", and is a bay (sinus) shaped enlargement of the postorbital and temporal canals connected with the ear labyrinth. Bramford calls this "peculiar structure" in *C. harengus* the "posterior dilation." He says it resides in the "temporal fossa" and has been called a fatty mass by some previous workers. He notes that it was also found in *C. pilchardus* by Wohlfahrt, and lies as a bag of water, with no flow through it, in direct connection with parts of the optic lobe of the brain, from which it is separated only by the *dura mater*. He suggests that it may act as a pressure organ.

Although Bramford speaks of the structure being open to the sea, he apparently refers to the pores of the supra-orbital and supra-temporal canals, and makes no reference to the numerous pores through which we pumped the cephalic line system with ink, which can be seen in Fig. 1 above and posterior to the eye. If this is one and the same

structure in the three clupeids (*Clupea pilchardus, C. harengus* and *Brevoortia*), it is certainly proportionally larger in *Brevoortia*, at least exteriorly. We have not made internal anatomical studies, which would require descriptions of the bones and other matters.

Specimens of *Brevoortia tyrannus* (Latrobe) of the Atlantic coast and *Brevoortia smithi* Hildebrand (of the Gulf and Atlantic coasts) and *Brevoortia gunteri* Hildebrand (of the Gulf coast) show similar cephalic lines. The two fine-scaled menhaden, *B. gunteri* and *smithi*, and the two large-scaled menhaden, *tyrannus* and *patronus*, have cephalic lines more similar to their cognates than to fishes of the other pair, but our examinations do not show discernible specific differences in this character.

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Gulf Coast Research Laboratory, Ocean Springs, Mississippi

Touch Receptors in Fishes with Special Reference to the Moray Eels (*Gymnothorax vicinus* and *G. moringa*)

John E. Bardach and Lois A. Loewenthal

TOUCH stimuli play a multiple role in the lives of fishes. First they serve for thigmotactic orientation and avoidance (Moehres 1941, Schiche, 1920) and secondly they may aid in the discrimination between palatable and unpalatable food objects (Bardach, Winn and Menzel, 1959).

Certain avoidance reactions are clearly mediated by the lateral line system (Dijkgraaf, 1934) while in others skin receptors are involved which react to touch as well as to currents (Jordan, 1917, Hoagland, 1933). Action potentials of cutaneous receptors in the barbels of the catfish, (*Ameirus* [=*Ictalurus*] *nebulosus*) supplied by the VII cranial nerve complex were recorded upon touch and the application of a jet of water but no detailed description of receptor anatomy was given. Wedell, Palmer and Pallie (1955) pointed out in a review article on nerve endings in mammalian skin that specific receptor function in any animal should only be ascribed to a specific structure upon electrophysiological evidence and that morphological studies of nerve terminals should be based on their functional (action potential) reactions to stimuli (mechanical thermal, chemical) rather than on taxonomic differences. It would indeed be desirable that not only mammalian but all sensory receptors and their nerves be investigated by electrophysiological means but for technical reasons one often has to proceed, albeit tentatively, on more circumstantial evidence.

Free nerve endings abound in the epidermis and in the corium of fishes and cyclostomes (Plate, 1924; and Krause, 1923). Dogiel, after Plate, (1924), described on the barbels of sturgeons an innervation from a single nerve outfall into the epidermis, dividing into a branch leading to sensory buds which resemble chemoreceptors and another branch which proliferates into a nerve net with free endings. Plate (1924) interpreted such a dual arrangement either to mean that the free endings respond to tactile and perhaps thermal stimuli while the buds are primarily taste receptors or that neither structure has specific

receptor functions but that buds and diffuse endings reinforce one another. Hoagland (1933) showed that catfish barbels, histologically similar to those of the sturgeon, responded to minimal touch or water currents as well as to chemical stimuli. Since the nature of the electric response to touch and chemicals differed in a nerve which carried a number of fibers from the barbel and since the sensory buds of fishes are similar to the chemoreceptors of other vertebrates one may agree with Herrick's interpretation (1901) that certain tactile receptors in *Ameirus* [=*Ictalurus*] are indeed free nerve endings. Apart from subserving touch, thermal sensations in fishes are also mediated by free nerve endings (Dijkgraaf, 1940, Bardach, 1956, Whitear, 1952).

There also exist in the corium of vertebrates structures of connective and nervous tissue which have been described as touch corpuscles. The corial touch receptors such as those treated by Meissner, Krause and Vater-Paccini in mammals and by Gaudry and Herbst in birds (Plate, 1924) have the following organization in common: A loosely bunched skein of nerve fibrils and endings is surrounded by a capsule of connective tissue.

Such mechanical design appears well suited for the detection of the slightest changes in the relative position of surrounding tissues, hence for pressure and touch discrimination and the specific function of these structures as highly localized receptors of small pressure and touch stimuli is generally accepted.

Among anamniotes such corpuscles have, so far, only been described from the pectoral fins of *Scyllium* (Wunderer, 1908). Loewenstein (1956) provided electrophysiological evidence that they function as proprioceptors and react to active and passive fin movements and deformations. Oppel (1900) suggested, without presenting evidence, that teleost fishes should have specialized and localized touch receptors and Bardach, Winn and Menzel (1959) surmized that certain dermal structures on the lips of moray eels indeed represented such a specialization. These structures have now been investigated in more detail; their histology and observations on the feeding behavior of the fish strongly imply that they indeed mediate the sensation of touch and that therefore specific touch receptors exist in teleost fishes, similar to those in higher vertebrates.

Materials and Methods

The manner in which moray eels located and ingested their food was observed on specimens kept in tanks at the Bermuda Biological Station for Research and experiments were performed which eliminated smell and taste stimuli (Bardach, Winn and Menzel, 1959). Strips of skin were taken from the inside of the mouth, from upper and lower lips and from the head at set distances terminating at the level of the opercular openings. The most common species of Bermuda morays were used, (*Gymnothorax vicinus* Caslelnau and *G. moringa* Cuvier) and nine to 15 micron sections were prepared following the silver protargol method of Bodian.

Observations and Results

Morays locate their food mainly by smell and appear to discriminate by taste and also by touch whether or not to ingest a given morsel. The fish are mainly active at night and "test" the food they come upon by touching it with lips or the tip of the jaws. They will also reject unpalatable objects such as paraffin-coated baitfishes on which they voraciously feed when the bait is not treated (Bardach, Winn and Menzel, 1959). Furthermore certain species of parrotfishes which secrete a mucous envelope at night are relatively immune from predation by morays (Winn and Bardach, 1958). Such discrimination in the absence of sight must rely on chemical senses and to some extent also on the touch or feel of the prey. The tip of the snout and the lips of the moray are rich in sensory structures which are receptors for both chemical and pressure or touch stimuli.

Taste buds are densest on the latero-distal edge of the lip; proceeding towards the edge of the lip both taste buds and corial or touch papillae are present. On the buccal surface of the lips and in the roof of the mouth only corial papillae occur. Nerves enter into the structures and form skein-like convolutions in their center (Fig. 1).

The presumptive touch structures, like the taste buds, are densest on the snout, less dense on the sides of the jaw and still less dense inside the mouth and towards the angle of the jaw. Neither presumptive taste nor touch structures could be found outside the lips on head or body. Their absence elsewhere but in the mouth and on the snout is not unexpected since the animal rests in caves and crevices and its mode of food searching is

Fig. 1. Lower lip of moray eel (*Gymnothorax moringa*) with taste buds and divergently oriented touch receptors; Bodian's Protargol Silver stain, low (100 ×) magnification.

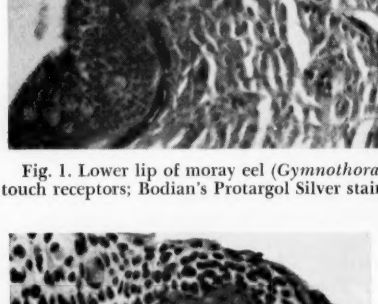

Fig. 2. Touch receptor of the moray eel from same region as Fig. 1, showing connective tissue envelope and coiled nerve fibers; Bodian's Protargol silver stain; high dry (440 ×) magnification.

such that it would come in first contact with food items with its head rather than its body.

External touch and pressure sensations from the body surfaces of lower vertebrates have been described as protopathic by Kappers, Huber and Crosby (1936) who suggested that this sense was relatively unrefined and based on the summation of impulses from many free nerve endings over large, rather than localized, areas. When fine or "epicritic" discriminations by touch can be made, specialized structures have evolved in certain areas of the body such as the lips and tips of extremities. Free nerve endings, however, also exist in the same regions and further add to the discriminatory capacities of the organism. Although we have only investigated two species of moray eels for the existence and distribution of touch corpuscles it is likely that specialized touch or pressure receptors can be found on other fish species, especially those which rely more on chemical senses than on vision for the finding of food.

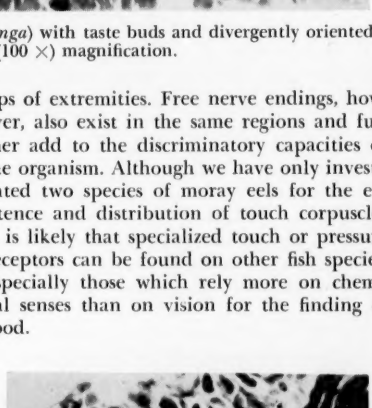

Fig. 3. Touch receptor from the roof of the mouth of the moray eel, showing crenulated connective tissue envelope, and straight nerve fibers. Bodian's Protargol silver stain; high dry (440 ×) magnification.

Touch corpuscle-like structures of the moray are composed essentially of a lamellated capsule of connective tissue with a core of "tactile cells." One or several nerve fibers enter the lower end of the corpuscle. The fibers give off branches which seem to terminate on and around the "tactile cells". Two varieties of corpuscles are seen in the moray eel: one is common to the lips, (Fig. 2) and the other is found only in the roof of the mouth (Fig. 3). These differ from one another in over-all orientation, in vascular pattern, in type of nerve convolution and in relationship to the epithelium.

The corpuscles of the lips have a random orientation with respect to the epidermal surface. Some are directly perpendicular to the surface while others extend into the epidermis at various angles. All of the corpuscles of the roof of the mouth, on the other hand, are perpendicular to the mucous membrane. In both cases the apices of the cortical papillae are covered with flattened epithelial cells continuous with the basal layer of the epidermis.

A blood vessel or capillary loop is seen extending well into each corial papilla in the roof of the mouth. In the papillae of the lips, however, blood vessels are usually seen only in the basal regions. In the lips, the nerve fibers appear to pursue a tightly spiral course, whereas in the roof of the mouth, the fibers are fairly straight.

A well-defined basement membrane separates corial papillae from epidermis. In the lips, this membrane is relatively thin and the junction between corium and epidermis is fairly smooth even where the papilla pushes into the epithelium. In the roof of the mouth the corpuscle-like structures assume the shape of a spiny knob extending into the epithelium. This spiny appearance is imposed by marked irregularity of a thickened basement membrane. The structural differences in the corpuscles relative to their location probaby do not reflect functional differences, but may possibly be accounted for by the fact that those of the roof of the mouth are found over a flat bony surface while those on the lips are in a more flexible environment.

Summary

1) Touch corpuscles, such as have been described from birds and mammals have, in lower vertebrates, so far only been found in sharks.

2) Feeding behavior of moray eels (higher fishes) implicated touch to play a role in the ingestion of food and a histologic examination of the moray's mouth region revealed two types of dermo-neural structures there which closely resemble the touch corpuscles previously described from amniotes.

3) The corpuscles consist of fine strands or skeins of nerves enveloped by connective tissue. They are densest on the lips towards the apex of the snout but also occur on the roof of the mouth. Their frequency of distribution roughly coincides with that of taste buds which are also present.

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DEPARTMENT OF FISHERIES AND DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN.

A new Gobioid Fish from the Antilles and Comments on *Ctenogobius fasciatus* and *C. curtisi*

C. RICHARD ROBINS AND JAMES E. BÖHLKE

CURRENT studies of several genera of tropical Atlantic gobioid fishes have exposed other problems of no direct concern to the genera in question. Varied data on these problems, including the description of a new genus and species, are assembled here. Giles W. Mead (Museum of Comparative Zoology, Harvard University), Yngve Löwegren (Lund University), Ernest A. Lachner (U. S. National Museum) and Loren P. Woods (Chicago Natural History Museum) loaned specimens or aided us during visits to their institutions. Victor G. Springer sent the specimen designated holotype below and allowed us to prepare the diagnosis of this species which he, too, recognized as new. This paper is an outgrowth of continuing studies on Bahaman and Florida shore fishes, studies variously supported by Mr. Charles C. G. Chaplin and the National Science Foundation (G-3881, G-9695). This paper was written while the senior author was at the Academy as a Jessup scholar.

Varicus gen. nov

The classification accorded gobioid fishes is by no means uniform. Attempts to separate two families, Eleotridae and Gobiidae, on the basis of divided or united ventral fins have resulted in unnatural groupings. Such species as those placed in *Eviota, Eviotops* and *Trimma* (all with divided ventral fins) appear to bear no direct relation to *Eleotris, Gobiomorus, Dormitator* and their allies but find instead closely similar species among the gobies with united ventral fins. Similarly, divergence between various lines of gobies with united ventrals appears greater than that between some groups that are now placed by many workers in two families, the Gobiidae and Eleotridae. We choose to place *Varicus* in the Gobiidae despite its nearly separate ventral fins. *Varicus* is superficially similar to *Cabillus lacertops* Smith (1959:207) but that species (and genus) has 6 dorsal spines and (from the illustration), branched ventral rays.

Ventral fins consisting of one spine and five simple rays, the fifth much reduced and adherent to the fourth. Interradial membranes reduced, the spine and four rays projecting as free fingers (see Fig. 1). Membrane uniting the ventral fins greatly reduced, almost absent, ventral frenum absent. Seven dorsal spines, the first five in a group, the sixth and seventh more distantly spaced. Body covered with large ctenoid scales, the head, nape, pectoral base, chest and midline of belly naked. Tongue bilobed to truncate. Head pores absent. Anterior nostrils tubular, the tubes moderate. Gill opening a vertical slit without an anterior leg. Rostral frenum absent, the mouth moderately protractile. No teeth on vomer or palatine bones. Jaw teeth multiserial, the outer row somewhat enlarged. Seventeen segmented caudal rays, 14 of them branched. Five branchiostegal rays, one on the ephihyal, three on the enlarged distal end of the ceratohyal and one on the shaft

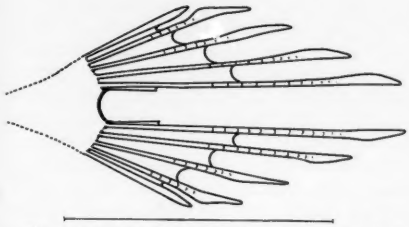

Fig. 1. Ventral fins of *Varicus bucca* based on the holotype, ANSP 93083, standard length 25.8 mm. Base line equals 5 mm.

ately behind preorbital rim. Posterior nostril remote from anterior, a simple opening just in front of eye in the smaller two specimens, but at the end of a short tube in the larger paratype. Tip of tongue deeply cleft, bilobate except in the larger paratype where the two lobes are fused and the anterior margin of the tongue nearly truncate. Teeth in upper jaw in a band about four teeth wide anteriorly, the outer series greatly enlarged. Teeth on lower jaw triserial anteriorly, uniserial behind; outermost series represented by

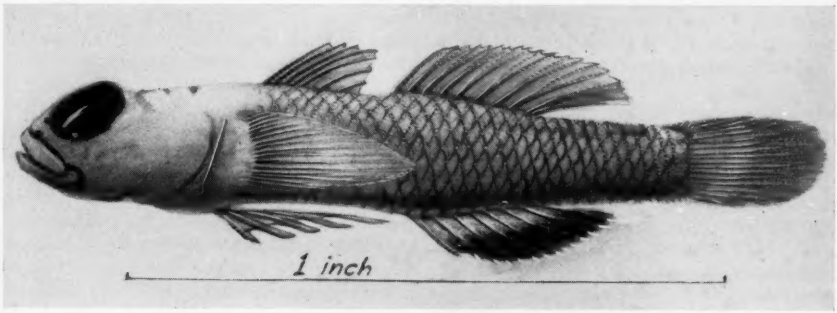

Fig. 2. Lateral view of holotype of *Varicus bucca*, ANSP 93083, S.L. 25.8 mm. Base line equals 1 inch.

of the ceratohyal. Some dorsal and anal soft rays and pectoral rays branched.

Generic type.—*Varicus bucca sp. nov.*

Varicus bucca sp. nov.

Fig. 1–3

Description.—(In the listing of body proportions the first figure applies to the holotype, the second to the larger paratype). Body short and somewhat compressed, its depth at dorsal fin origin .190 (.190) standard length. Least depth of caudal peduncle .132 (.119) S.L. Head large, .337 (.318) S.L., somewhat depressed, its greatest depth .193 S.L. and greatest width (measured across opercles) .229 (.254) S.L. No nuchal crest present. Eyes large, prominent, elliptical; horizontal eye diameter .116 (.107) S.L., nearly twice the snout length and when projected caudad, reaching the upper end of the gill opening. Interorbital very narrow, its least bony dimension less than one-fourth diameter of pupil. Snout short, obtuse. Mouth terminal, gape but slightly diagonal. Posterior end of maxillary below middle of eye. Anterior nostril with a moderate tube, placed immediately three or four enlarged teeth anteriorly on either side. Innermost series consisting of five or six greatly enlarged teeth extending back nearly half way on the jaw; central row composed of numerous close-set tiny teeth extending back to the angle of the gape. No teeth in roof of mouth. Gill opening but little longer than the pectoral base, curved,

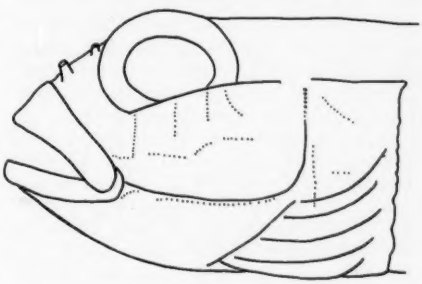

Fig. 3. Lateral view of head of *Varicus bucca* showing distribution of sensory papillae. Illustration composite but based on the paratype CNHM 65608, S.L. 40.2 mm. Base line equals 5 mm.

but the lower end not extending far forward nor does the opening leave free an angular flap at its postero-ventral angle. Gills four. Seven gillrakers present from angle to anterior limit of lower arm. All rakers short and stubby, the first, at the angle, slightly longer. Inner edge of shoulder girdle without fleshy cirri or papillae. No spine on the preopercle. Cutaneous papillae on head low and poorly defined, present only on the cheeks, opercles and along the sides of the throat. The paths and extent of the various papillar tracts vary somewhat between specimens and even between the two sides of the same fish. The general arrangement of papillae is diagrammed in Fig. 3.

Dorsal: VII,10. Anal: 8. Pectorals: 18/19 (18/18, 16/17 in the larger and smaller paratypes respectively).

No dorsal spine prolonged, the second through fifth subequal in length. First five spines equally spaced, the sixth twice as far from the fifth as the fifth is from the fourth and the seventh even more distant from the sixth. First element in second dorsal and anal fins a spine, and last ray in each fin split to its base. Dorsal fins well separated, the space between them one-third to one-half the length of the base of the first dorsal fin. Origin of anal fin below the interspace between elements two and three of the second dorsal fin. Both second dorsal and anal fins, when depressed, falling far short of caudal base; second dorsal extending farther caudad than anal. The last seven dorsal rays and all anal rays (except the first) branched. Pectoral fins pointed, the longest ray .264 (.246) S.L. and reaching back to above the origin of the anal fin; all pectoral rays branched. Ventral fins I,5/I,5, their shape as in figure 2. Membrane connecting the two ventral fins reduced to a low basal ridge. Longest (fourth) ventral ray .252 (.353) S.L. Caudal fin rounded, with 17 segmented rays of which the two uppermost and the lowermost are unbranched.

Scales in a horizontal series between end of pectoral-fin base and base of caudal 27, scales around caudal peduncle 12. Four scales form a basal sheath on the caudal fin; of these, the middle two are like the body scales, but the upper and lower scales have enlarged and curved lateral denticles. These denticles are shortest at the free tip of the scale, becoming progressively longer toward its base; these modified outer basicaudal scales are like those of *Chriolepis* and some other gobies, notably *Garmannia* and its allies. Body scales generally ctenoid the ctenii best developed on caudal-peduncle scales and posterior areas of the body, somewhat weaker on scales along the base of the dorsal and anal fins. Scales on belly cycloid or nearly so, gaining ctenii laterally. Scales behind pectoral fin cycloid or with few ctenii, the ctenii becoming stronger and more numerous posteriorly.

Coloration in alcohol.—Body, dorsal, caudal and paired fins unmarked in holotype. Dorsal spines and rays with gray spots, two or usually three per element in the large paratype. Outer two-thirds of anal-fin membrane (except for the margin) densely covered with melanophores, the entire fin appearing dusky at first glance. Head pale but with scattered melanophores on the cheeks and occiput. Melanophore arrangement on occiput suggesting three bands in the holotype, the bands distinct in the larger paratype. The three bands not straight but winged shaped, the anterior one shortest, the posterior one longest. A patch of melanophores present on cheek, behind eye, another on upper part of opercle. Body somewhat dusky above, unmarked below, the melanophores concentrated near scale margins especially anteriorly. Dusky pattern extends forward to axil of pectoral fin partially enclosing a pale middorsal area that extends as a rectangle from the origin of the spinous dorsal fin to the pallid nape and occiput. This pale rectangle crossed anteriorly by a dusky band in the larger paratype.

Apparently the pattern does not develop in small specimens for the smaller paratype and holotype are largely unmarked.

Holotype.—ANSP 93083, a female, 25.8 mm. in standard length, from Saba Bank between St. Kitts, British West Indies and St. Croix, Virgin Islands, Lat. 17° 33′ N., Long. 63° 35′ W., 125–132 fathoms, September 25, 1958, M/V *Oregon*, Station 2356, 40-foot flat trawl.

Paratypes.—CNHM 65608, an adult female with enlarged ovarian eggs, 40.2 mm. S.L., north of Culebra Island, Lat. 18° 29′ N., Long. 65° 13.5′ W., 28 fathoms, September 29, 1959, M/V *Oregon*, Station 2677, 40-foot flat trawl. USNM 143022, a juvenile in poor condition, 19.2 mm. S.L., from off Habana, Cuba, Lat. 23° 10′ 54″ N., Long. 82° 17′ 45″ W., 115 fathoms, January 17, 1885, steamer *Albatross*, Station 2322.

After this paper went to press an additional specimen, also designated paratype was received from Mr. Harvey R. Bullis, Jr. of the U. S. Fish and Wildlife Service. This specimen, UMML 7114 (1,46.3) is from Lat. 18°

29′ N., Long. 65° 13.5′ W. in 28 fms., M/V *Oregon*, Station 2627, September 29, 1959. It has VII, 9 dorsal, 8 anal and 18/18 pectoral rays and had a vertically elongate dusky blotch on each side under the base of the last dorsal ray.

Name.—Varicus, meaning "with feet spread out", alluding to the form of the ventral fins; *bucca*, "the puffed cheek", here treated as an appositional noun.

Ctenogobius fasciatus Gill

Although many workers, particularly those working on Indo-Pacific fishes, have cached various species of gobies in *Ctenogobius*, such action is without foundation. Gill (1858:376, 430) described *Ctenogobius fasciatus* from Trinidad. By the title and comments in the introduction to his paper and by associating this goby entirely with species known to inhabit fresh water, Gill indicates that his *Ctenogobius fasciatus* is from fresh or at most brackish water. The generic type of *Ctenogobius* has not been recognized since its original description; all subsequent references to *fasciatus* can be referred to other forms. In his later paper on Trinidad fishes, Regan (1906: 392) identified four specimens as *Gobius fasciatus*. These specimens were shown by Ginsberg (1932:15) to be *Gobionellus claytoni* (Meek), an action overlooked by subsequent workers (*e. g.*, Boeseman 1960:139).

Eigenmann and Eigenmann (1888:62–3) based their discussion of *fasciatus* on MCZ 13231, a specimen from Haiti. This specimen is at hand. Its counts are: dorsal: VI,12; anal: 13; pectorals: 17/18; segmented caudal: 17; lateral scales about 40. Also, the nape is unscaled and there is no canine tooth on the lower jaw. The Eigenmanns erroneously listed the fin-ray counts. We reidentify this specimen as *Gobionellus claytoni*.

Rosén (1911:63) reported *Gobius fasciatus* from Stanniard Creek on Andros Island, Bahamas. His specimen, 21.5 mm. in standard length, also examined by ûs, has 11 second dorsal and 12 anal rays and approximately 30 lateral scales. Apparently it had no predorsal scales and no dark shoulder blotch, but the specimen is both faded and very brown. It is here identified as *Gobionellus boleosoma* (Jordan and Gilbert).

The six specimens, USNM 156653 6, 15.7–35.7 mm. S.L.) reported on by Beebe and Tee-Van (1928:222) are in poor condition and it is particularly difficult to determine accurately the scale counts. Either *Gobionellus claytoni* or *G. stigmaticus* is represented. On the basis of the absence of a shoulder spot, a vertical bar on the cheek and the absence of a canine tooth on the side of the lower jaw we assign this record to *G. claytoni*.

Ctenogobius fasciatus Gill is thus still known only from the original account (compiled accounts excepted), the type lost. Gill (1858:376) listed counts of *fasciatus* as "V.11. A.10. . . . P.13." He subsequently noted (1863: 263) that there were six dorsal spines, the "V" resulting from an error in typography. These counts, coupled with other features of the description, are diagnostic (if correct) and stymie the identification of *fasciatus* with any other American goby known to us. Particularly cogent is the greater number of dorsal than anal rays. As already noted authors have particularly identified with *fasciatus* species of *Gobionellus*, notably *claytoni*, probably because of the elongate dark lateral dashes that juveniles of this species possess. But all species of *Gobionellus* have one more anal than second dorsal element except for rare variants which have equal numbers of both. More thorough survey of brackish waters on Trinidad and adjacent South America may yield new material. Meanwhile, *Ctenogobius fasciatus* must be considered *incertae sedis* and other species placed in *Ctenogobius* rest on uncertain foundation.

The only other Western Atlantic goby currently in *Ctenogobius* is *C. curtisi* Fowler (1952:108–9, figs. 8–9) described from a specimen collected at Port-au-Prince, Haiti. The type, ANSP 72128, was restudied. Data noted are: dorsal: VI,10; anal: 11; segmented caudal. 17; pectorals: 17/17; standard length 38.6 mm. The peculiar jaw teeth and the scaled occiput are particularly diagnostic. The type is a male, with prolonged dorsal spines and with several recurved teeth without notches forming a short inner second row anteriorly. The teeth on the upper jaw are uniserial and like those of the outer row on the lower jaw have notched tips. The pair of basicaudal spots so characteristic of *Evorthodus* is present. This nominal species is clearly to be added to the already extensive synonymy of *Evorthodus lyricus* (Girard). For a discussion of *E. lyricus* and its synonymy see Ginsburg (1931).

In the eastern Pacific, Eigenmann (1917: 685; 1922:214–15, pl. 29, fig. 2) described *Gobius daguae* from the Río Dagua of Colombia, and placed it in the subgenus *Ctenogobius*. This species is a *Gobionellus* and it needs comparison with *G. manglicola* (Jordan

and Starks), for the two apparently have similar fin-ray and scale counts.

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The Marine Laboratory, University of Miami and Chaplin Chair of Ichthyology, Academy of Natural Sciences of Philadelphia.

Chionodraco markhami, a New Antarctic Fish of the Family Chaenichthyidae[1]

Richard Gordon Miller and John Reseck, Jr.

During the austral summer of 1959 the junior author accompanied the New Zealand Oceanographic Institute's cruise of HMNZS ENDEAVOUR in the Ross Sea (Bullivant, 1959). We thank the Ross Dependency Research Committee of New Zealand, the Committee on Polar Research, and the U. S. National Committee for the International Goephysical Year of the National Academy of Sciences, Washington, for arranging our participation and support, the Arctic Institute of North America for sponsorship and services, Scripps Institution of Oceanography, California Academy of Sciences, and the Sport Fishing Institute for equipment.

Of the several unknown fishes among the 92 specimens obtained (Miller, 1961; Reseck, 1961), one species is described herein as new. It is based on two specimens falling within the genus *Chionodraco* but distinct from the previously described forms. In naming a new species we take pleasure in acknowledging the interest and support of Dr. G. W. Markham, Director of the New Zealand Department of Scientific and Industrial Research and his staff in the Institute of Oceanography, Wellington.

Chionodraco markhami, sp. nov.
Fig. 1

Holotype.—A male 297 mm. in standard length taken at Station A460, 75° 38′ S., 168° 32′ E., approximately 24 miles north of Franklin Island, 17 January, 1959. It was taken in a 4-foot beam trawl at a depth of 415–430 meters over a bottom of gritty mud. It is assigned museum number 2963 in the Dominion Museum, Wellington, New Zealand.

Paratype.—A male 274 mm. in standard length, taken at Station A459, 75° 17′ S, 172° 20′ E, approximately 75 miles northeast of Franklin Island, 16 January 1959. This specimen was taken by trawl in 290 fathoms, over

[1] Contribution of the New Zealand Oceanographic Institute, Wellington; Paper No. 5, of the Fisheries Laboratory, Long Beach State College, and Foresta Institute Paper No. 3.

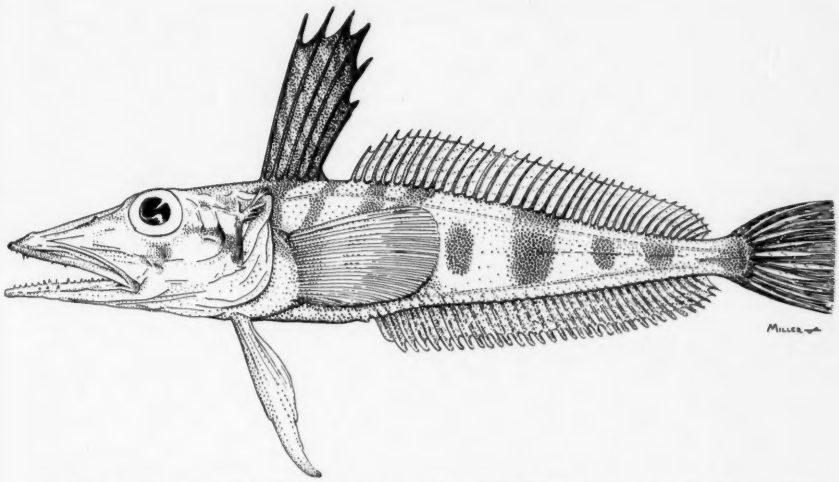

Fig. 1. *Chionodraco markhami* sp. nov. Holotype from HMNZS *Endeavour* Ross Sea Station A460; standard length 297 mm. (Author's drawing.)

soft mud. It is desposited in the US National Museum with a number 179895.

Description.—Proportions of the two new specimens, paratype in parentheses, are as follows: depth of body 5.5 (7.1) in standard length; length of head 2.8 (2.7) in standard length; diameter of eye 4.7 (4.5) into head length; bony interorbital width 4.3 (4.3) in head length. Snout slightly less than half the length of head. Maxillary extending below anterior border of eye. Lower jaw protruding, both jaws bearing an inner and outer row of well-spaced canine teeth, those of the inner row more numerous and curved inward. A series of minute papillae, dusky at tips, rim the jaws. Tongue present and well formed in the holotype, but in the paratype (and in our specimens of *Chionodraco kathleenae* and *Cryodraco antarticus*) the tongue lacks definition, possibly because of distension of jaws and gill covers. Gillrakers reduced to 4 and 5 (5 and 6) slight protuberances at the angle of the first arch. Rostrum long, bony, without spines, and bearing a single pair of nostrils which are located ¾ of the distance from tip of snout to eye. The upper angle of the opercle, which represents the terminus of the head, a spatulate flap extending beyond the bony tip which is composed of four spines. The lighter pigmentation of part of the opercular membrane suggests it may be partially folded under in life. Preopercle bearing a spine at angle of the subopercle with a small spinelet on the outer margin. Six strong branchiostegal rays present. These and the gill-covers broadly distended with the mouth agape. Opisthotony is a general condition in chaenichthyids. Pseudobranchae present.

Body naked, with three lateral lines consisting of tubes, the pores of which are directed variously upward or downward along the line as in our examples of *Chionodraco kathleenae*. Upper lateral line extending from above operculum to end of soft dorsal, formed of a series of 72–73 scales, originating above 5th anal ray, and extending nearly to end of base of anal fin. Middle lateral line composed of about 6–9 tube-scales, occurs on the caudal peduncle proximal to the mid-caudal ray. Dorsal VI,37 (VI,38); anal 35 (35); pectoral I-21 (I-20); ventrals I-5 with mid-ray longest, 1.6 (1.4) in head, 4.3 (3.8) in standard length. The dorsal spines not markedly rigid or pungent, but rather flexible.

Measurements in thousandths of standard length are given in Table 1 for the two types and for the two representatives in our collection of the nearest relative, *Chionodraco kathleenae*. In Table 2 data for the new species are compared with those for *C. kathleenae* Regan and *C. hamatus* (Lönnberg) as provided by Norman (1938).

Pattern and color similar to that of *Chionodraco kathleenae*. Head a dusky yellowish tan, with darker patches on maxillary, snout and mandible, at the nostrils, over and below the eye, behind the eye and a diagonal blotch from eye across preopercle to lower portion of opercle. Five large blotches saddling the body, interspaced with smaller blotches, one at the

TABLE 1. PROPORTIONS OF *Chionodraco markhami* AND *C. kathleenae* IN THOUSANDTHS OF THE STANDARD LENGTH.

	Chionodraco markhami			*Chionodraco kathleenae*		
	Holotype EN70	Paratype EN40	Mean	EN64	EN68	Mean
Standard length	297 mm	274 mm		263 mm	260 mm	
Length of head	368	372	(370)	390	396	(393)
Depth of head	169	186	(177.5)	196	189	(192.5)
Length of snout	169	168	(168.5)	190	189	(189.5)
Postorbital length	121	124	(122.5)	133	134	(133.5)
Snout to nostril	121	128	(124.5)	141	142	(141.5)
Diameter of eye	81	84	(82.5)	76	77	(76.5)
Interorbital	88	84	(86)	106	104	(105)
Length of maxillary	188	197	(192.5)	208	212	(210)
Length of mandible	178	182	(180)	212	212	(212)
Depth of body at dorsal	188	168	(178)	205	212	(208.5)
Least depth of peduncle	44	44	(44)	42	46	(44)
Snout to origin of dorsal	358	360	(359)	372	377	(374.5)
Snout to origin of anal	515	515	(515)	570	578	(574)
Snout to origin of pectoral	376	380	(378)	420	424	(422)
Snout to origin of ventral	323	344	(333.5)	384	392	(388)
Anal to last caudal vertebra	485	475	(480)	415	427	(421)
Dorsal origin to anal origin	175	184	(179.5)	236	261	(248.5)
Base of spinous dorsal	94	88	(91)	74	88	(81)
Base of soft dorsal	470	475	(472.5)	460	470	(465)
Base of anal	440	420	(430)	392	368	(380)
Height of spinous dorsal	254	234	(244)	144	154	(149)
Height of 3d dorsal ray	85	88	(86.5)	88	85	(86.5)
Height of anal	67	73	(70)	80	85	(82.5)
Interdorsal space (spine-ray)	54	44	(49)	74	77	(75.5)
Length of pectoral	222	218	(220)	232	223	(227.5)
Length of ventral	236	258	(247)	278	295	(286.5)
Length of caudal (median ray from last vertebra)	135	135	(135)	144	158	(151)

TABLE 2. *Chionodraco markhami* COMPARED WITH NORMAN'S 1938 DATA FOR *C. kathleenae* REGAN AND *C. hamatus* (LÖNNBERG)

	C. markhami		*C. kathleenae*	*C. hamatus*
	EN70	EN40		
Depth of body in standard length	5.5	7.1	5–6.25	—
Eye diameter* in length of head	4.7	4.5	4.75–6.25	4.6 (5 in young)
Interorbital width in length of head	4	4.3	3.5–4	3.4
Length of head in standard length	2.8	2.7	2.6–3	—
Dorsal fin	VI,37	VI,38	V–VIII,38–45	VII,37
Anal fin	35	35	34–38	33
Pectoral fins	I,21	I,20	22–24 (I,21–I,23)	—
Length of ventral fin in head	1.6	1.4	1.25–2	2

(Regan 1914, and Lönnberg 1905)

* Norman (1938) calls attention to apparent variations of body proportions in different sizes of a species. His notes on disproportional growth of the spinous dorsal, the ventrals, eye, and snout must be kept in mind in drawing conclusions from the few known specimens.

axil of the pectoral, one a pectoral's length along the body, and one at the base of the caudal. Fins all dusky, the rays notably darker than the membrane, ventrals and anal lighter than dorsal and pectorals. First dorsal blackish throughout. Peritoneum dusky. In paratype the pattern is essentially the same, but more strikingly accentuated and with markings of sides merging into one long blotch.

Both examples are males with large gonads.

Discussion.—The genus *Chionodraco* is part of the group of socalled "bloodless fishes" which are lacking (Ruud, 1959) or relatively without (Andriashev, 1959, Martsinkevitch, 1958) red blood cells. *C. markhami* appears to be no exception, being "whiteblooded," though blood analysis is not yet under way.

Configuration and proportions of our specimens approximate those of *Chionodraco kathleenae* Regan (1914, p. 13) as presented by Norman (1938, p. 78–79). However, *C. markhami* is certainly distinct from *C. kathleenae*, as shown in the extreme height of its spinous dorsal, the relatively forward position and greater length of the anal fin, the longer mandible, the shorter snout and head, and the narrower interorbital. From X-ray photographs our holotype appears to have 56 (at most 58) vertebrae compared to 64 in *C. kathleenae* (Norman, 1938). Our new species differs from *C. hamatus* in the narrower interorbital, greater number of anal rays and longer ventral fins. From all the others of the genus ours differs in the lack of a rostral spine.

KEY TO THE KNOWN SPECIES OF *Chionodraco*

1. Distance from snout to first dorsal fin 1.6 or more in distance between symphysis and origin of anal fin; height of first dorsal 5–7 in standard length; rostral spine present.
   a. Pelvic fins long, extending beyond vent (nearly three-quarters the length of head); eye small, 4.75–6.25 in length of head . . . . . *C. kathleenae*
   b. Pelvic fins short, not extending beyond vent (one-half the length of head); eye large, 4.66 in length of head . . . . . *C. hamatus*
2. Distance from snout to first dorsal fin 1.4 or less in distance between symphysis and origin of anal fin; height of first dorsal 4 in standard length; rostral spine lacking . . .

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LONG BEACH STATE COLLEGE AND FORESTA INSTITUTE FOR OCEAN AND MOUNTAIN STUDIES, CARSON CITY, NEVADA.

Two New Butterflyfishes (Family Chaetodontidae) of the Indo-Pacific Genus *Forcipiger*[1]

JOHN E. RANDALL

THE unique butterflyfish genus *Forcipiger* Jordan and McGregor, previously known only from the wide-ranging *F. longirostris* (Broussonet)—a species noted for its absurdly long and slender snout—is reviewed in the present paper. Two new species are described, both with even longer snouts than *longirostris*.

Specimens were examined in collections of the United States National Museum (USNM),

[1] Contribution No. 296 from The Marine Laboratory, University of Miami.

American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Scripps Institution of Oceanography, and the University of California, Los Angeles. James E. Böhlke of the Academy of Natural Sciences of Philadelphia loaned specimens of *Forcipiger* which were catalogued after the author's visit to this institution. William A. Gosline of the University of Hawaii (UH) and Robert R. Rofen of the George Vanderbilt Foundation (GVF), Stanford University, loaned specimens of one new species which were collected by the author. Michio Takata of the Division of Fish and Game in Hawaii provided two additional specimens. Robert H. Kanazawa of the United States National Museum and Vladimir Walters of the American Museum of Natural History provided collection data for types of the second new species. Walter Courtenay of The Marine Laboratory, University of Miami, took an X ray picture of specimens of the three species of *Forcipiger* for vertebral counts which is on file in the Division of Fishes of the United States National Museum. Carl L. Hubbs of the Scripps Institution of Oceanography reviewed the manuscript.

In the Indo-Pacific there are three closely related genera of chaetodont fishes with prolonged snouts: the monotypic *Chelmo* Oken of the Indo-Malayan region, monotypic *Chelmonops* Bleeker of Australia, and *Forcipiger*. *Prognathodes aculeatus* (Poey) of the West Indies possesses a produced snout, but this species appears to have developed its long snout independently, probably as an offshoot from a form like *Chaetodon aya* Jordan, which it resembles (Hubbs and Rechnitzer, 1958).

The differentiation of *Forcipiger* from *Chelmo* and *Chelmonops* needs clarification. Fowler and Bean (1929:45) wrote of *Forcipiger*, "Related to *Chelmo* and *Chelmonops* but differing from both in the greatly longer high spinous dorsal, spines 12 or 13." This is not entirely true. The longest dorsal spine of *Forcipiger* is contained 3.3 to 4.3 times in the standard length (s.l.), that of *Chelmo* about 3.9, and that of *Chelmonops* 4.5. A better distinction with respect to the spinous portion of the dorsal fin is to note which of the spines are the longest. The longest dorsal spine of *Forcipiger* is the fifth; the longest dorsal spines of *Chelmo* and *Chelmonops* are the most posterior ones. Also, the spinous portion of the fin is scaled only basally in *Forcipiger*, but is about two-thirds covered with scales in *Chelmo* and *Chelmonops*.

Weber and de Beaufort (1936:15) distinguished *Forcipiger* and *Chelmo* in a key, with number 1 applying to *Forcipiger* and 2 to *Chelmo*, as follows:

1. Velvet-like band of minute teeth in jaws. Dorsal XII–XIII, 22–23. Pectorals long, falcate.

2. Teeth small, pointed, forming several brushlike bands. D IX, 26–31. Pectorals rather short, acutely rounded.

Upon examination of the teeth of these two genera, I see no distinction as given. They each have a mass of close-set, small, conical teeth in which bands are difficult to distinguish. The length of the teeth does not differ materially in the two genera. The patches of teeth are slightly more extensive in *Chelmo*. The dentition of *Chelmonops* is comparable.

Although dorsal spine counts effect separation of *Forcipiger* and *Chelmo*, they do not distinguish *Forcipiger* from *Chelmonops*, which has XI spines. Counts recorded for the dorsal spines of *Forcipiger longirostris* by the author were all XII except for the single specimen from Madagascar and one of five from Baja California both of which have XI (Table 1). Although no specimens with XIII spines were found, it is likely that occasional ones exist, for this count is recorded not only by Weber and de Beaufort but also by Smith (1949:236). The two new species of *Forcipiger* have X or XI dorsal spines.

The length of the pectoral fin is a satisfactory key character for the genus *Forcipiger*. The pectoral fin length is contained about 2.5 times in s.l. in *Forcipiger* and about 4 times in *Chelmo* and *Chelmonops*.

Body depth is another distinguishing character. The depth is contained an average of about 2.3 times in s.l. of *Forcipiger*, 1.9 in *Chelmonops* and 1.6 in *Chelmo*.

Chelmonops may be further separated by its shorter snout, about 2.4 in head length. Snout lengths of *Forcipiger* and *Chelmo* are contained less than 2 times in the head length (except for a variant of *Chelmo rostratus* (Linnaeus) from northern Australia in which the snout is about 2 in head length).

Forcipiger may be characterized as follows: body strongly compressed (width 4 to 6 in head length) and high (depth 2.0 to 2.7 in s.l.). Snout tubular and enormously produced, mostly by prolongation of premaxillaries and mandibles, its length 2.6 to 4.5 in s.l. No spines on head except for a broad-based, flattened projection at hind edge of opercle. Opercular membrane well developed. Mouth small and terminal. Teeth minute and close-

TABLE 1. FIN-RAY COUNTS OF SPECIES OF *Forcipiger*

Species and Locality	Dorsal Rays										Anal Rays				Pectoral Rays		
	X	XI	XII	21	22	23	24	25	26	27	III	17	18	19	15	16	17
longirostris																	
Hawaiian Islands	—	—	34	1	5	22	4	2	—	—	34	13	19	2	—	30	4
East Indies, Philippines	—	—	25	—	7	15	3	—	—	—	25	9	16	—	2	22	1
Marshall Islands	—	—	6	—	2	2	2	—	—	—	6	2	4	—	—	6	—
New Hebrides	—	—	2	—	—	2	—	—	—	—	2	—	2	—	—	2	—
Samoa	—	—	1	—	—	1	—	—	—	—	1	—	1	—	—	—	1
Society Islands	—	—	2	—	—	1	1	—	—	—	2	1	1	—	—	2	—
Revillagigedo Islands	—	—	5	—	2	3	—	—	—	—	5	1	4	—	—	5	—
Clipperton Island	—	—	1	—	—	1	—	—	—	—	1	—	1	—	1	—	—
Baja California	—	1	4	—	—	4	1	—	—	—	5	1	4	—	3	2	—
Madagascar	—	1	—	—	—	1	—	—	—	—	1	1	—	—	—	1	—
inornatus																	
Hawaii	1	2	—	—	—	—	—	1	1	1	3	—	1	2	—	3	—
Tuamotu Archipelago	—	1	—	—	—	—	—	—	1	—	1	—	—	1	—	1	—
cyrano																	
East Indies	—	3	—	—	—	—	—	—	3	—	3	—	2	1	2	1	—
Solomon Islands	—	1	—	—	—	—	—	1	—	—	1	1	—	—	—	1	—

set in a broad band in jaws. Profile of head posterior to snout very steep. Mid-dorsal region of nape a moderately sharp ridge. Lateral line highly arched, following contour of back, terminating at base of caudal fin. Scales small, ctenoid, from 61 to 78 in lateral line. Dorsal fin elevated, scaled on about the basal fourth of spinous portion (with projections of scales extending upward alternately on left and right sides of spines). Dorsal fin with from X to XIII stout spines and 21 to 27 soft-rays. Fifth dorsal spine the longest, its length 3.3 to 4.3 in s.l. Membranes between dorsal spines excised nearly to base anteriorly, progressively less notched posteriorly, until between the last two spines the notch extends downward from tip of preceding spine a distance equal to one-fifth to one-sixth the length of last spine. Anal fin with III stout spines and from 17 to 19 soft-rays. Margins of soft portion of dorsal and anal fins are nearly vertical to base of caudal fin. Pectoral rays 15 to 17; pectoral fins long, their length from 2.3 to 3.4 in s.l. Pelvic rays I,5; pelvic fins long, the first ray reaching to or beyond base of second anal spine; scaled axillary process present. Caudal fin emarginate, with 17 principal rays. Gill membranes attached to isthmus. 11 abdominal and 13 caudal vertebrae (including hypural complex).

KEY TO THE SPECIES OF *Forcipiger*

(Based on specimens in excess of 70 mm s.l.)

1a. Length of snout 3.6 to 4.5 in standard length; gape (tip of snout to rictus) 1.3 to 3.4 in eye diameter; median band of scales on interorbital broad, the width ½ to ⅔ of interorbital space; preopercular margin serrate, especially near angle; dorsal with XI to XIII (usually XII) spines and 21 to 25 (usually 23 and rarely 21 or 25) rays ..... *longirostris*

1b. Length of snout 2.6 to 3.0 in standard length; gape 4.3 to 6.0 in eye diameter, median band of scales on interorbital narrow (consisting of a single row of scales anteriorly), the width ⅓ or less of interorbital space; preopercular margin smooth; dorsal with X or XI spines and 25 to 27 soft rays 2

2a. Color in preservation dark brown; lateral line scales 67 to 71 ..... *inornatus*, n. sp.

2b. Color in preservative light yellowish brown with head above eye and pectoral base abruptly dark brown and a dark brown spot posteriorly on anal fin; lateral line scales 61 to 63 ..... *cyrano, sp. nov.*

Forcipiger longirostris (Broussonet)

Figs. 1, 2, 6A

Chaetodon longirostris Broussonet 1782, Ichth. Decas, 1: no pagination; if pages after introduction are counted, account of this species appears on pp. 23–26 and a figure on pl. 7.

Chelmon longirostris Cuvier 1831, Hist. Nat. Poiss., 7:89.

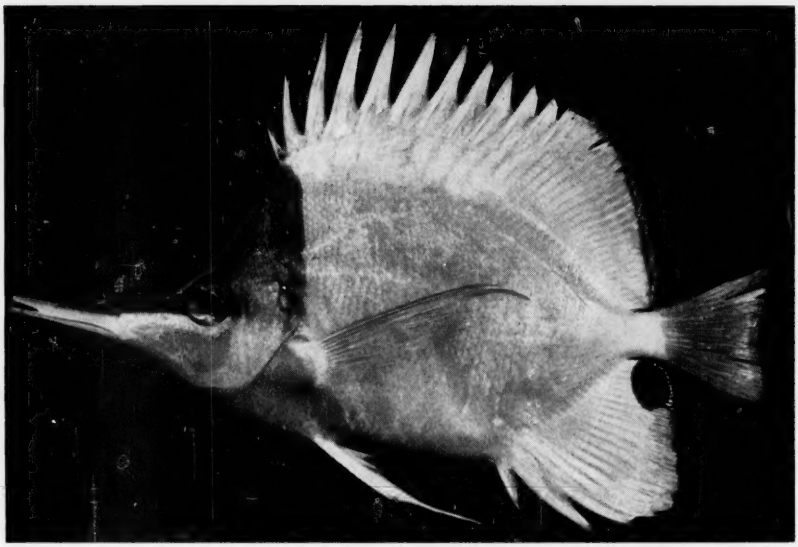

Fig. 1. *Forcipiger longirostris* (Broussonet), ANSP 71369, standard length 125 mm, New Hebrides.

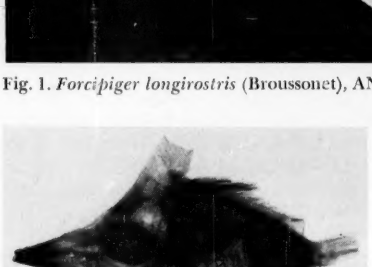

Fig. 2. Late postlarval or *Tholichthys* stage of *Forcipiger longirostris*, USNM 65838, standard length 16.5 mm, surface south of Fakarava, Tuamotu Archipelago. Occipital spine broken. Photo by C. E. Cutress.

Chelmon lol Montrouzier 1856, Ann. Sci. Phys. Nat. Soc. Agric. Lyon, 8:444.

Forcipiger flavissimus Jordan and McGregor *in* Jordan and Evermann 1898, Bull. U. S. Natl. Mus., 47(2):1671.

Type Locality.—Pacific Ocean, near the Society Islands and Hawaiian Islands.

Diagnosis.—Length of snout 3.6 to 4.5 in standard length; gape 1.3 to 3.4 in eye diameter; broad band of scales on interorbital; preopercular margin serrate, especially near angle; D XI–XIII (usually XII), 21–25; A III, 17–19 (rarely 19); P 15–17 (usually 16); lateral line scales 68–78; gillrakers 15–20 (in 12 specimens, mostly from Hawaii). Color in preservative light yellowish brown, the nape and head above a horizontal line passing through lower quarter of eye dark brown (except on interorbital region); a prominent black spot on outer posterior part of anal fin; no median dark brown band on interorbital space.

Color from a 35 mm. Kodachrome transparency of a fresh 75 mm. specimen collected by the author in the Marshall Islands: body bright yellow; nape and upper half of head black, the lower half and thorax white; fins yellow except caudal which is dusky hyaline; outer posterior part of soft portion of dorsal fin whitish with submarginal dark line; a comparable but more restricted whitish distal region posteriorly on anal fin; a large black spot on anal fin.

Discussion.—Jordan and McGregor *in* Jordan and Evermann (1898:1671–2) and Jordan and McGregor (1899:279) described *Forcipiger flavissimus* from the Revillagigedo Islands off western Mexico. They considered this species "extremely close to *F. longirostris*", and differentiated it on the basis of a deeper body and a larger, vertically oblong anal spot (as opposed to a round spot on *longirostris*). I was unable to notice any obvious difference in the spot on the anal fin between two paratypes of *flavissimus* in the United States National Museum and specimens of *longirostris*. The anal spot is not ocellated in *longirostris* as claimed by Jordan and McGregor. The body depth of *flavissimus*, however, is slightly

TABLE 2. COUNTS OF LATERAL-LINE SCALES OF SPECIES OF *Forcipiger*

Species and Locality	Lateral Line Scales																	
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
longirostris																		
Hawaiian Islands	—	—	—	—	—	—	—	—	3	2	4	4	4	3	1	3	—	1
East Indies, Philippines	—	—	—	—	—	—	—	1	2	5	2	1	2	1	—	—	—	—
Marshall Islands	—	—	—	—	—	—	—	1	—	2	1	1	1	—	—	—	—	—
Eastern Pacific	—	—	—	—	—	—	—	2	1	1	1	1	3	1	—	—	—	—
inornatus																		
Hawaii	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—
Tuamotu Archipelago	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
cyrano																		
East Indies	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Solomon Islands	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

greater than *longirostris*. The depth of the two paratypes (82 and 118.5 mm. in s.l.) and three large specimens (149.5 to 168 mm.) from the same island group is contained 1.98 to 2.0 in s.l. Four other Eastern Pacific specimens from Baja California and Clipperton Island have body depths from 2.0 to 2.2 in the standard length. Twenty-five specimens of *longirostris* from the East Indies and Hawaiian Islands (77 to 156.5 mm.) have body depths from 2.1 to 2.45 in the standard length (average 2.27). In view of the similarity in other characters, however, *flavissimus* should be referred to the synonymy of *longirostris*, as has been done previously by Jordan and Seale (1906:336), Fowler and Bean (1929:46–8), and Weber and de Beaufort (1936:17). *F. longirostris* is one of the few tropical Indo-Pacific fishes to have crossed the Eastern Pacific Barrier (Ekman, 1953; Randall, 1956:178).

The population of *F. longirostris* in the Hawaiian Islands appears to be racially differentiated on the basis of slightly higher counts of lateral line scales (Table 2). There is also a suggestion that the species grows to larger size in Hawaii. The mean size of 34 specimens from the Hawaiian Islands is 125.5 mm. s.l. Ten of these specimens are 140 mm. or more in s.l.; the largest measures 156.5 mm. Twenty-five specimens from the East Indies and Philippines average 108 mm. in s.l.; the largest is 140.7 mm. Six from the Marshall Islands range from 75 to 100 mm. in s.l., with a mean of 87.8. One of these, a 96-mm. specimen, is a ripe female. The apparent larger size in Hawaii may not be genetically controlled. Many fishes in Hawaii are known to attain larger size there than in more tropical localities, probably because of cooler water (for a discussion of the larger size of the surgeonfish *Acanthurus triostegus* in cool-water areas, see Randall, 1956:178). The largest *F. longirostris* seen among the collections examined was a 168 mm. specimen from Clarion Island in the Revillagigedos, a relatively cool-water locality.

Fowler and Bean (1929:47–8, fig. 2) stated that there is great variation in the relative length of the beak of specimens of *F. longirostris* from Oceania. However, these authors examined material of two species, *longirostris* and *cyrano*, the latter with a significantly longer snout. Actually, over the size range of specimens available to Fowler and Bean, the snout length of *longirostris* is fairly uniform relative to standard length, as may be seen in the graph of Fig. 3.

The extremely long snout and small mouth of *Forcipiger* suggest that the species may have very specific food requirements, but this was not confirmed by examination of the stomach contents of two specimens of *F. longirostris* from San Lucas Canyon, Baja California. These specimens were collected by R. H. Rosenblatt, C. Limbaugh, and R. J. Krejsa on March 26, 1959, and were examined later by the author, A. W. Ebeling, and others of the Scripps Institution of Oceanography. A 113.5-mm. specimen contained several mysid shrimps, fish eggs, barnacle cirri, and the tips of sabellid worm tentacles. An 85-mm. one had eaten several small polychaete worms (roughly 70 percent by volume) and numerous tips of sabellid worm tentacles (about 15 percent by volume). The remaining soft detrital material was not identified. Obviously, many more fresh specimens are needed for a satisfactory food habit study. But the data from these two specimens does serve to in-

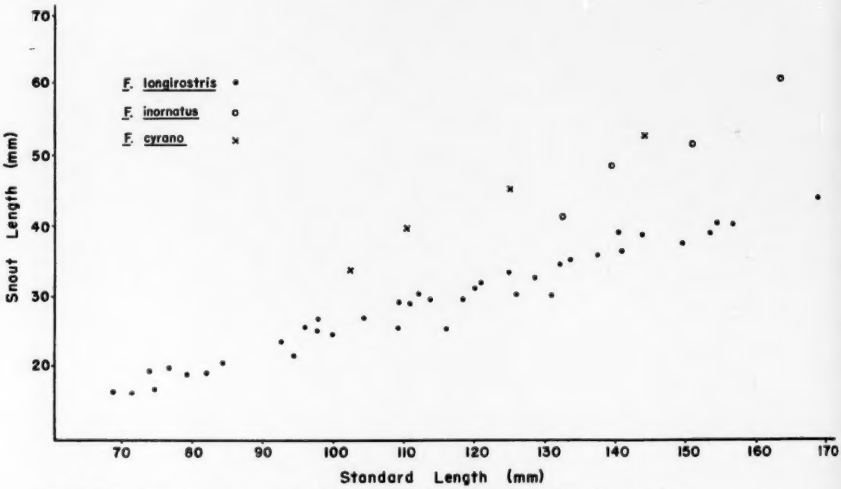

Fig. 3. Relationship of snout length to standard length of species of *Forcipiger*.

dicate that a variety of small organisms can be expected from *longirostris* stomachs.

Weber and de Beaufort (1936:18) gave the range of *F. longirostris* as the east coast of Africa, Madagascar, and Mauritius to China and throughout the Pacific to the islands of Clarion and Socorro. They stated that the species was "... everywhere rare and wanting in many intermediate localities f.i. in India." Although *longirostris* certainly remains to be recorded from many lesser areas, it is not rare in all known localities. It might be better to say that it is nowhere abundant. In the present paper the range is extended to western Mexico based on recent collections of the Scripps Institution of Oceanography and to Clipperton Island where a single 68.5 mm. specimen was taken by W. J. Baldwin of the University of California, Los Angeles. The author sighted *longirostris* underwater at Nuka Hiva in the Marquesas, a region from which the species is not yet recorded, but collected no specimens.

Forcipiger inornatus, *sp. nov.*

Figs. 4, 6B

Holotype.—USNM 179881, female, standard length (s.l.) 151 mm., collected with a spear by M. Takata off Keahole Point, Hawaii, at a depth of 35 feet over rock bottom with some coral on April 27, 1960.

Paratype.—USNM 179882, male, s.l. 139.5 mm., same collection data as holotype.

Paratype.—UH 2312, female, s.l. 163.7 mm., collected with a spear by J. E. Randall in Kealakekua Bay, Hawaii, at a depth of about 20 feet on June 14, 1954.

Paratype.—GVF 1325-2, Stanford University, male, s.l. 132.5 mm., collected with a spear by J. E. Randall outside of the reef just north of the pass of the atoll of Tikahau, Tuamotu Archipelago, at a depth of from 60 to 110 feet on June 14, 1957.

Description.—(data in parentheses are the extremes in counts and measurements for the three paratypes when differing from the holotype): dorsal ray X (XI), 26(25–27); anal rays III,19 (18–19); pectoral rays 16; gillrakers 16 (15–17); lateral line scales 69 (67–71); scale rows above lateral-line to origin of dorsal fin 12 (11); scales above lateral line to and including mid-dorsal row on caudal peduncle 6 (6–7); a single median row of scales anteriorly on interorbital space broadening to a band of about 5 scales in width over center of eyes and continuing to broaden posteriorly; median predorsal scales about 50 (40–42); median preventral scales about 27 (26–28); scales extend onto soft portion of dorsal and anal fins about two-thirds fin height anteriorly and about one-half fin height posteriorly.

Head length 1.85 (1.83–1.89), body depth 2.31 (2.30–2.56), snout length 2.90 (2.70–3.03), eye to origin of dorsal fin 4.95 (4.91–5.82), eye to origin of pelvic fin 4.74 (4.36–4.73), eye to origin of anal fin 2.42 (2.42–2.63), length of pectoral fin 3.03 (2.83–3.22), length of pelvic fin 3.60 (3.41–3.58), length of pelvic spine 6.60 (6.34–6.62), length of caudal fin 5.25 (5.37)

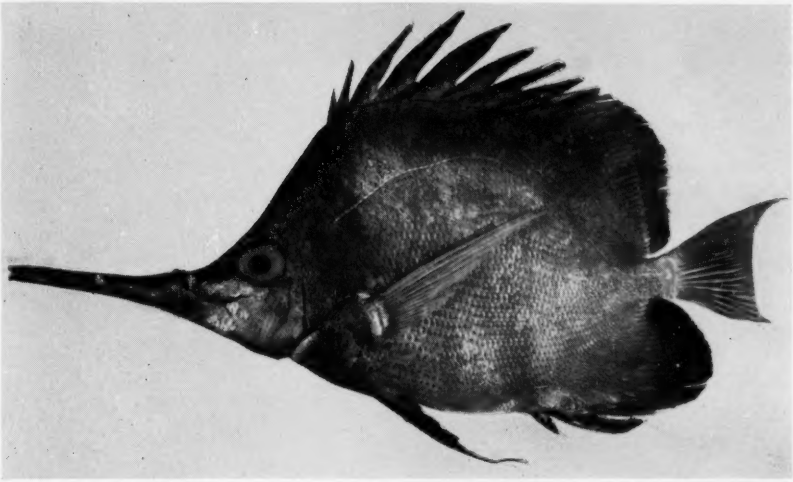

Fig. 4. *Forcipiger inornatus*, holotype, USNM 179881, standard length 151 mm, Hawaiian Islands.

(fin damaged on two paratypes), length of longest (fifth) dorsal spine 4.06 (4.10–4.18), length of first dorsal ray 5.25 (5.36–5.60), length of third anal spine 4.95 (4.57–4.95), length of first anal ray 5.03 (4.36–5.11)—all in s.l. (calculated, not stepped).

Maximum width of body (above pectoral fin) 5.15 (4.86–5.69), diameter of eye 7.24 (6.37–7.90), postorbital length of head 4.70 (4.47–5.11), width of interorbital space (over center of eye) 8.13 (7.78–8.90), least depth of caudal peduncle 8.05 (7.78–8.95)—all in head length.

First dorsal spine 4.32 (4.41–4.81), second dorsal spine 2.45 (2.38–2.61), third dorsal spine 1.27 (1.19–1.35), last dorsal spine 1.31 (1.20–1.38)—all in fifth dorsal spine. Spines posterior to fifth progressively shorter. Posterior soft-rays of dorsal progressively shorter than anterior rays, the last ray 3.26 (3.04–3.38) in first dorsal soft-ray. First anal spine 2.19 (2.12–2.22) and second anal spine 1.11 (1.12–1.13) in third anal spine. Last anal soft-ray 3.71 (3.64–4.05) in first anal soft-ray. Caudal fin emarginate, the upper lobe longer than the lower; caudal concavity (horizontal distance from end of upper lobe of fin to ends of median caudal rays) 4.43 (4.96) in length of fin.

Mouth very small, the gape 5.1 (4.7–6.1) in eye diameter. Jaws with a broad band of setiform teeth which are not arranged in regular rows (but about five teeth in depth at front of jaws, fewer on sides). The teeth are conical and slightly incurved, those at the front of the jaws of the holotype measure about 0.3 mm. (half this length imbedded in jaw tissue). Preopercular margin smooth, the angle broadly rounded.

Color in preservative dark brown, the centers of the scales on the body darker than the edges, resulting in a faint longitudinal banding which is more evident ventrally; head and body anterior to a vertical at level of base of third dorsal spine darker than rest of body; base of caudal and pectoral fins paler than rest of body; membranes of these fins hyaline, the rays dark-edged.

Color from a 35-mm. Kodachrome transparency of a Hawaiian specimen photographed immediately after capture by the author: body yellowish brown; head, nape, and breast dark brown; extreme base of pectoral and caudal fins yellow, rays brown, membranes hyaline; dorsal, anal, and pelvic fins dark brown.

Discussion.—Gosline and Brock (1960:9, 24) remarked on melanistic examples of *F. longirostris* in the South Kona area of the island of Hawaii and to old individuals of this species becoming plain blackish. These authors had probably observed specimens of *F. inornatus* which may appear black underwater. None of the larger specimens of *longirostris* examined by the author have shown a tendency to darken.

Charles C. G. Chaplin informed the author that he observed a long-snouted, coal-black butterflyfish (and hence probably *inornatus*) about 5 inches long at a depth of 180 feet

Fig. 5. *Forcipiger cyrano*, holotype, USNM 181373, standard length 143.3 mm, East Indies.

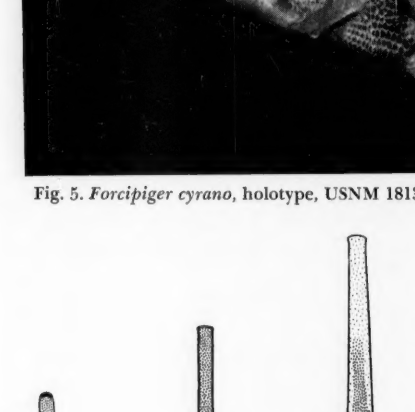

Fig. 6. Dorsal view of head of species of *Forcipiger*. A. *longirostris*, standard length 125.5 mm. B. *inornatus*, standard length 132.5 mm. C. *cyrano*, standard length 143.3 mm.

one-half mile south of Kailua on the Kona coast of Hawaii on August 21, 1959.

The holotype is a ripe female with a rotund ovary 24 mm. in length, the bulk of which consists of about 0.3-mm. ova. The 139 mm. paratype collected at the same time is a male. The two fish were observed swimming together as a pair by Takata before he speared them. The 163.7-mm. paratype is a ripe female.

The stomachs of the paratypes contained the crushed remains of small caridean shrimps (thirty about 3 to 10 mm. long in the 139.5-mm. paratype, eleven about 4 to 8 mm. long in the 163.7 mm. paratype, and six estimated to have been 3 to 6 mm. long in the Tuamotu paratype).

Forcipiger cyrano, *sp. nov.*

Figs 5, 6C

Forcipiger longirostris Fowler and Bean 1929 (in part), Bull. U. S. Natl. Mus. 100(8): 45–48, fig. 2.

Holotype.—USNM 181373 (linen tag 4767), female, standard length (s.l.) 143.3 mm., taken with dynamite by the Albatross Expedition at Malibagu Point, Celebes, East Indies, at a depth of 10 to 20 feet on November 21, 1909.

Paratype.—USNM 181374 (linen tag 4726), female, s.l. 125.4 mm., taken with dynamite by the Albatross Expedition at Buka Buka Island, Gulf of Tomini, Celebes, at a depth of from 5 to 15 feet on November 20, 1909.

Paratype.—AMNH 16584, female, s.l. 101.8 mm., collected by Otis Barton at Tanamerah Bay 50 miles west of Hollandia, New Guinea,

in late 1944. A 100-mm. specimen of *Forcipiger longirostris* was collected at the same locality.

Paratype.—USNM 169774, sex not determined, s.l. 110.5 mm., taken with dynamite and rotenone by W. M. Chapman on the outer reef of Wana Wana Island, Blackett Strait, New Georgia, Solomon Islands, on June 24, 1944.

Description.—(data in parentheses are the extremes in counts and measurements for the three paratypes when differing from the holotype): dorsal rays XI,26 (25–26); anal rays III, 18 (17–19); pectoral rays 15 (15–16); gillrakers 16 (16–18); lateral line scales 63 (61–63); scales above lateral line to origin of dorsal fin 10; scales above lateral line to and including middorsal row on caudal peduncle 6; a single median row of scales anteriorly on interorbital space (extending to nostrils on paratypes) which broadens to five scales in width over center of eyes; median predorsal scales about 33 (43–51); median preventral scales about 24 (23–25); scales extend onto soft portion of dorsal and anal fins about two-thirds fin height anteriorly and about one-half fin height posteriorly.

Head length 1.83 (1.81–1.86), body depth 2.61 (2.23–2.64), snout length 2.70 (2.76–2.97), eye to origin of dorsal fin 5.29 (4.55–5.48), eye to origin of pelvic fin 4.86 (4.63–5.14), eye to origin of anal fin 2.41 (2.51–2.64), length of pectoral fin 3.28 (tip broken in holotype) (2.67–2.90), length of pelvic fin 3.19 (3.10–3.30), length of pelvic spine 6.50 (5.90–6.30), length of longest (fifth) dorsal spine 4.42 (blunt on holotype) (3.48–4.00), length of first dorsal soft-ray 5.72 (4.51–5.29), length of third anal spine 4.79 (3.94–4.23), length of first anal soft-ray 4.53 (3.78–4.00)—all in s.l. (calculated, not stepped). Caudal fins damaged on all specimens; therefore lengths not given.

Maximum width of body 5.37 (5.37–5.85), diameter of eye 7.93 (6.30–7.24), postorbital length of head 5.13 (4.57–5:13), width of interorbital space (over center of eyes) 8.26 (6.95–8.40), least depth of caudal peduncle 8.45 (7.12–8.39)—all in head length.

First dorsal spine 4.98 (4.17–4.32), second dorsal spine 2.86 (2.16–2.44), third dorsal spine 1.85 (1.12–1.22), eleventh dorsal spine 1.33 (1.32–1.37)—all in fifth dorsal spine. Spines posterior to fifth progressively shorter. Posterior soft-rays of dorsal fin progressively shorter than anterior rays, the last 3.14 (3.63–3.94) in first dorsal soft-rays. First anal spine 2.19 (2.28–2.56) and second anal spine 1.22 1.23–1.25) in third anal spine. Last anal soft-ray 3.92 (4.72–4.55) in first anal soft-ray. Caudal fin slightly emarginate, with the upper lobe slightly produced.

Mouth very small, the gape 4.31 (4.13–4.65) in diameter of eye. Jaws with a broad band of small setiform teeth not arranged in regular rows; about 8 teeth in depth on upper jaw and 4 or 5 on lower at front (fewer on sides) (jaws damaged on holotype). Teeth conical and slightly incurved, those at front of jaws of holotype about 0.4 mm. in length (half of this length imbedded in jaw tissue). Preopercular margin smooth, the angle broadly rounded.

Color in preservative light yellowish brown, with a large triangular dark-brown area on head and nape anterior to a vertical from origin of dorsal fin to base of pectoral fin and dorsal to a line of demarcation running through lower edge of eye; top of head with an elongate light yellowish brown spindle-shaped area which includes all of interorbital space; a median dark-brown band bisecting anterior half of pale area on forehead; top of tubular portion of snout dark brown, more densely pigmented proximally; a round dark-brown spot, about two-thirds as large as eye on approximately the outer half of last five to six anal soft-rays; margin of soft portion of dorsal and anal fins pale with a submarginal dusky band about half as broad as pale margin at its widest point.

Doubtful Specimen.—USNM 181372 (linen tag 4811), a 104-mm. specimen collected by the Albatross Expedition at Powati Harbor, Makyan Island, Philippine Islands, on November 28, 1909.

This fish is like the specimens of *cyrano* described above except for its shorter snout (snout length 29 mm. — a length which would fit the graph line of *longirostris* in Fig. 3), steeper profile of head, and 24 dorsal soft-rays. Although it is probably a specimen of *cyrano*, more material is needed to ascertain if it is aberrant or a Philippine variant.

Discussion.—Forcipiger cyrano probably escaped detection in the field and among museum collections as a distinct form because it so closely resembles *longirostris* in color pattern. The most significant color difference of these two butterflyfishes is the presence on *cyrano* of a median black band extending forward from the interorbital space and the absence of this marking on *longirostris* (Fig. 6). In spite of the similarity of the color patterns of these species, *cyrano* appears to be

more closely related to *inornatus* than to *longirostris*, as may readily be noted from the key and descriptions. Were it not for color, *cyrano* and *inornatus* would be difficult to differentiate. Although lateral line scale counts effect separation (Table 2), additional counts might result in an overlap of the ranges of the counts for the two species.

F. cyrano and *F. inornatus* are well separated geographically with respect to the localities where they have thus far been collected. The former is known from the Indo-Malayan and Melanesian regions, the latter from eastern Oceania.

The stomach of the 101.8-mm. paratype from New Guinea contained 13 caridean shrimp, none entire, which ranged in length from about 3 to 10 mm. The stomach of the 110.5-mm. paratype from the Solomons contained three mysid shrimps 3.5 to 8 mm. long of the genus *Siriella* (identified by Thomas E. Bowman of the U. S. National Museum) and one crab megalops.

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Marine Laboratory, University of Miami, Miami, Fla.

Description of a New Genus and Species of Tree Frog from South America

Coleman J. Goin

When Professor J. Eiselt of the Natural History Museum of Vienna forwarded his Colombian frogs to me for study, he included a number of uncatalogued tree frogs from various South American localities for identification. While unpacking them, I noticed one little hylid that on subsequent examination proved to be so trenchantly different from any hylid so far known that I feel the only satisfactory treatment is to set it off in a separate genus.

Habrahyla, *gen. nov.*

Type species.—Habrahyla eiselti, sp. nov.

Diagnosis.—A hylid with vertical pupils; tongue bilobed and free behind; rounded sacral diapophyses; unapposable thumb; derm free of skull and roof of skull not exostosed; teeth present only on the upper jaws and vomers; palpebral membrane not reticulate; webbing reduced on hands and feet.

It differs from all hylid genera except *Triprion, Nyctimantis, Nyctimystes, Phyllomedusa* and *Agalychnis* by its vertical pupil. From *Triprion* it differs in lacking parasphenoid teeth and a proboscis, in having the cranial derm free and in having the tongue bilobed and free behind. From *Nyctimantis* it differs in having the cranial derm free and in having the tongue extensively free behind. From *Phyllomedusa, Agalychnis,* and *Nyctimystes,* it differs in having the tongue distinctly rather than weakly bilobed behind, in having the sacral diapophyses rounded rather than greatly expanded; and from *Nytimystes* and all *Agalychnis* except *cal-*

Fig. 1. Dorsal view and side view of head of the type of *Habrahyla eistelti*.

carifer by the lack of reticulations on the palpebral membrane. From both *Phyllomedusa* and *Agalychnis* it differs in having a shorter, stouter body with a broad flat head, in pattern formation, and in coloration.

Habrahyla eiselti, *sp. nov.*

Fig. 1, 2

Type.—Natural History Museum, Vienna, No. 16454, adult male, collected in Brazil.

Diagnosis.—As for the genus.

Description of type.—Vomerine teeth in two small, rounded mounds, lying close together between the small, rounded choanae, a single tooth in the left mound, two teeth in the right; tongue one-third as wide as mouth-opening, elongate, its posterior border extensively free and with a pair of well developed posterior horns; snout short, U-shaped when viewed from above, truncate in profile, the upper jaw not extending appreciably beyond lower; nostrils lateral, slightly projecting, their distance from end of snout about one-half that from eye, separated from each other by an interval equal to about their distance from eye. Canthus rostralis well defined; loreal region concave and nearly vertical, the upper lip flaring out but slightly below it. Eye large, very prominent, its diameter nearly twice its distance from nostril; palpebral membrane not reticu-

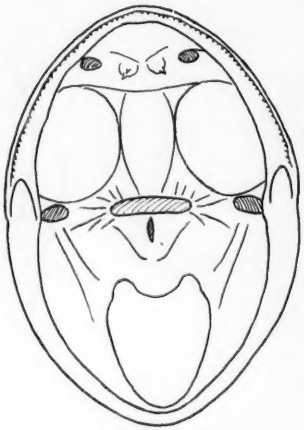

Fig. 2. View of inside of mouth of type of *Habrahyla eiselti*.

late; pupil vertical; interorbital distance slightly greater than width of upper eyelid, which is relatively wide and slightly greater than distance between nostrils. Tympanum distinct, about one-third the diameter of eye, separated from eye by a distance about equal to one-third its own diameter. Fingers with a trace of web at base, fourth considerably longer than second, reaching to middle of disk of third which covers about one-half the tympanic area; no projecting rudiment of a pollex; no ulnar ridge; toes about one-third webbed, the web on fourth toe reaching base of antepenultimate phalanx; fifth toe about one disk longer than third; first toe distinctly shorter than second; disk of fourth covering about one-third the tympanic area; a very distinct oval inner and a smaller indistinct, rounded outer metatarsal tubercle; no tarsal ridge; no dermal appendage on heel. Body not elongate, in post-axillary region less than greatest width of head; when hind leg is adpressed, heel reaches almost to nostril; when limbs are laid along the side, knee and elbow very slightly overlap; when hind legs are bent at right angles to body, heels fit snugly together. No patagium extends from the back of the upper arm to the side of the body. Skin of upper parts smooth; a rather indistinct, very narrow glandular ridge encircling upper part of tympanum; skin of throat and chest smooth, that of belly and lower surface of thigh uniformly and very finely granular; no apparent traces of a skinfold across chest; adult male, vocal sac not apparent externally. Skin of head not coossified with skull, roof of skull not exostosed.

Dimensions.—Head and body 24.2 mm.; head length 10.0 mm.; head width 10.7 mm.; femur 12.0 mm.; tibia 12.4 mm.; heel-to-toe 16.1 mm.; hand 8.2 mm.

Color in alcohol.—Dorsal ground color a dark bluish-gray, ventral ground color a cadaverish gray. A narrow white line margins the upper lip, the ulnar side of each hand and arm to the elbow and the lateral side of each foot to the heel. There is on each elbow, knee, and heel a most conspicuous clear white spot. Along the sides of the body the dark dorsal ground color merges gradually with the paler color below with no sharp line of demarcation.

Discussion.—From the diagnosis it would seem that this new genus is closest to *Phyllomedusa* but I suspect that the similarities may be in part due to convergence. When I first saw this frog, I took it to be a distinctive little *Hyla*. The general aspect is more like that of *Hyla* than like that of any other hylid genus. It was only when I looked at it closely that I realized it had characters in common with *Phyllomedusa*.

Not only is the build quite different from that of a phyllomedusid, but the pattern is distinctive as well. While phyllomedusids have their bright markings, if present, on the concealed surfaces, in *Habrahyla eiselti* the concealed surfaces are somber and the bright light spots on the exposed surfaces of the elbows, knees, and heels stand out vividly.

Since this single specimen is all the material that is now available, I wanted to keep dissection to a minimum. I therefore had X-ray photographs made to study the internal bony structure. These X-rays confirmed that the sacral diapophyses are rounded rather than flat and expanded as in *Phyllomedusa*. No bony sternum or omosternum can be seen.

The structure of the tongue is distinct from that of any hylid except the phyllomedusids. It is quite free posteriorly and has better developed posterior horns than any *Phyllomedusa* or *Agalychnis* I have seen.

The vomerine teeth are also distinctive. The vomerine patch on the left consists of a fleshy mound of tissue from which protrudes a single, rather broad, triangular-shaped tooth. On the right the situation is similar except that a smaller (replacing?) tooth can be seen deep and anterior to the large, triangular-shaped tooth. It is tempting to speculate

that a single vomerine tooth on each side might be characteristic of this genus.

I hesitated for some time before deciding on the advisability of erecting a new genus on the basis of a single specimen without precise locality data. However, this frog is so strikingly different from any so far known that it would seem to me to be even worse to return it to Vienna to sit unidentified and perhaps unnoticed on a shelf. I believe that calling attention to it in the hopes that other workers will watch for additional specimens fully justifies a description based on this limited material.

Professor Eiselt informs me that the original catalogue gives no clue as to additional data for the specimen.

I am indeed grateful to Professor Eiselt for the privilege of reporting on this specimen; to Miss Esther Coogle for the fine sketches that accompany this description; to Mr. Wayne King for making an X-ray photograph for me; and to the National Science Foundation for the grants (NSF-G5628 and NSF-G13325) to further my studies of South American tree frogs.

SUMMARY

A new genus and species of hylid frog, *Habrahyla eiselti*, is described from Brazil. It shows several similarities to *Phyllomedusa* (e.g., vertical pupil) but its exact relationship cannot be determined at present.

DEPARTMENT OF BIOLOGY, UNIVERSITY OF FLORIDA, GAINESVILLE, FLORIDA.

A New Genus of Lungless Salamander from the Coastal Plain of Alabama

RICHARD HIGHTON

A REMARKABLE salamander was recently collected in southern Alabama by Mr. Leslie Hubricht and sent to the United States National Museum. Through the courtesy of Dr. Doris M. Cochran, the writer has had the opportunity to examine the specimen, which represents an undescribed species so different from its closest relatives that a new genus is here proposed for it.

The new salamander is related to the genera *Desmognathus* and *Leurognathus*, which occupy a somewhat isolated position in the Plethodontidae. Dunn (1926) included both genera in this family, unlike most earlier workers, who had placed them in a separate family, the Desmognathidae. Soler (1950:460–1) presented a historical résumé of the familial status of these genera. Smith and Taylor (1948:16) and Soler (*op. cit.*) maintained that the family Desmognathidae should be recognized, but their classification has not been followed by all herpetologists. Some have considered the two genera in question as a subfamily of the Plethodontidae, the Desmognathinae. In the opinion of the writer, the differences between these two genera and the other lungless salamanders are not as great as those between other families of salamanders. Therefore a subfamily status for the desmognathines is more in accordance with the present classification of the Caudata. Since the new form is clearly related to *Desmognathus* and *Leurognathus*, its familial status is the same as theirs, and need not be considered further in this paper.

The status of the doubtful genus *Haptoglossa* from Costa Rica, based on a single specimen, now lost, has been discussed by Dunn (1926:429), Taylor (1944:229–30; 1952: 748–9) and Soler (1950:474). According to Cope (1893:334–5), the specimen of *Haptoglossa pressicauda* had a tongue attached in front, unlike all other Central American salamanders of the family Plethodontidae, but otherwise was similar to them. It is extremely unlikely, on both morphological and geographic grounds, that the present form could be *Haptoglossa*.

The new form differs from all other species of desmognathines in its large size, elongated body and short legs. The body form and reduced legs indicate that it is a burrowing species and this may account for the fact that it has eluded discovery in spite of intensive collecting in the southeastern United States. It has 22 trunk vertebrae and 21 costal grooves, while all the known species of *Des-*

mognathus and *Leurognathus* possess a modal number of 15 trunk vertebrae and 14 costal grooves. Only rarely do specimens of the other desmognathines possess one more or less body segment than the modal number. In *Desmognathus* and *Leurognathus,* the number of intercostal folds between the toes of the adpressed limbs varies from one to six (Bishop, 1943), while there are 13 in the new short-limbed form. The light bar from the eye to the angle of the jaw, characteristic of all known species of *Desmognathus,* is absent. There has been no reduction in the number of toes or in the number of phalanges in spite of the reduced size of the legs and feet.

Since only a single specimen of the new form has thus far been taken, variation within the species is unknown. An X-ray photograph has been taken (figure 1), but some important aspects of the skull are obscure and the procurement of additional material must be awaited before it will be possible to compare certain osteological features of the new form with those of *Desmognathus* and *Leurognathus.*

Phaeognathus, *gen. nov.*

Generic type: *Phaeognathus hubrichti*

Diagnosis.—A plethodontid with four toes on the front feet, five on the hind feet; tongue attached in front and in the middle; maxilla normal; vomerine and paravomerine teeth not continuous; occipital condyles stalked; terminal phalanges T-shaped; no palmar tubercles; very short limbs, with 13 intercostal folds between the toes of adpressed limbs; 22 trunk vertebrae (21 costal grooves) and 44 tail vertebrae; no light bar from posterior angle of the eye to the angle of the jaw; internal nares normal; tail with slight keel; tail not constricted at base.

From the radiograph, it is clear that *Phaeognathus* has stalked occipital condyles like those of *Desmognathus* and *Leurognathus.* The vertebrae appear to be opisthocoelous. It is not possible to determine the condition of the premaxillae or prefrontal from the X-ray photograph. A fontanelle is present between the fused premaxillae in *Desmognathus,* but absent in *Leurognathus. Phaeognathus* would be expected to possess a fontanelle, since only the completely aquatic *Leurognathus* has a reduced internasal gland (Dunn, 1926:19). The prefrontals may be absent, since they do not occur in *Desmognathus* and *Leurognathus.* Black pigment is present in the walls of the cloaca, unlike all other desmognathines. The heads of preserved specimens of *Desmognathus* and *Leurognathus* are bent downward in a unique manner (Soler, 1950:470). The head of the specimen of *Phaeognathus* is bent downward in the same way, indicating that its anterior musculature is similar to theirs. The new form appears to possess the same modified atlas and temporal muscles that keep the lower jaw immobile as in the other two closely related genera. Vomerine teeth num-

Fig. 1. X-ray photograph of holotype of *Phaeognathus hubrichti.*

ber 9 and 11 on a side in the female holotype, more than in any other species of desmognathine with the exception of *D. quadramaculatus*. The vomerine tooth rows form a "V" with the two rows meeting posteriorly just in front of the separate paravomerine patches of teeth, similar to the condition in a female *D. fuscus* figured by Bishop (1941: fig. 3i). There is a slight depression separating the vomerine and paravomerine teeth. Since the only available specimen of *Phaeognathus* is a female, it is not known whether the vomerine teeth of adult males are lost or reduced, as they are in some of the larger species of *Desmognathus* (*monticola, planiceps, fuscus* and *ochrophaeus*). The vomerine teeth of adults of both sexes are lost in some populations of *Leurognathus marmorata*, but only in the larger males of other races (Martof, 1956). The snout-vent length and the tail length of the specimen of *Phaeognathus hubrichti* are much greater than any other known desmognathine.

Phaeognathus hubrichti, *sp. nov.*

Holotype.—USNM 142486, a female, collected three miles northwest of McKenzie on U. S. Route 31, Butler County, Alabama, on June 18, 1960, by Leslie Hubricht.

Diagnosis.—Since only one species of the genus is known, its diagnostic characters must be the same as those for the genus.

Description of the holotype.—Head length (snout to gular fold), 20 mm.; head width at widest point (behind eye), 12 mm.; snout to anterior angle of vent, 101 mm.; snout to posterior angle of vent, 107 mm.; total length, 221 mm.; length of anterior limbs, 11 mm.; length of posterior limbs, 14 mm. (right) and 15 mm. (left). Toes on hind feet (in order of increasing length) 1–5–2–4–3; toes on front feet, 1–4–2–3. The webbing on the toes of the fore limb extends to the joint between the first and second phalanges; on the hind limb only half the distance of the first phalanx. The color, after two months preservation, is uniformly dark brown dorsally and ventrally except for a few small light spots on the sides and feet that may have been occupied by white pigment in life. The vomerine teeth number 9 on the right and 11 on the left. The oviducts appear to be mature, but there are no large eggs in the ovaries. The specimen is not recently spent, so it may be just beginning to mature. A photograph of the holotype is shown in figure 2.

The specimen of *Phaeognathus hubrichti* was collected by Mr. Hubricht under leaves in a wooded area on the slope of a ravine. Further field work in the region will be of great interest, not only in order to obtain additional material for morphological study, but also to learn something about the habits and life history of *Phaeognathus*, the first new genus of salamanders discovered in the United States since 1939. The discovery of this novelty in the Coastal Plain is surprising since the center of distribution of the subfamily is in the Appalachian Mountain region. The only other species of desmognathine salamander known from the southern

Fig. 2. The type specimen of *Phaeognathus hubrichti*.

Coastal Plain of Alabama is *Desmognathus fuscus*.

Summary

A plethodontid salamander from Butler County, Alabama, represents a new genus and species, described herein as *Phaeognathus hubrichti*. The new genus is related to *Desmognathus* and *Leurognathus*, which it resembles in possessing similar head musculature, stalked occipital condyles, and probably also opisthocoelous vertebrae. It differs from the other two genera of the subfamily Desmognathinae in possessing seven more body vertebrae, reduced limbs and a greater size.

Acknowledgements.—The writer wishes to thank Mr. Hubricht and Dr. Cochran for permission to describe this form and the National Science Foundation for financial support of this research. Mr. Robert Kanazawa kindly took the radiograph. Misses Anne Moskos and Hannah Segal made a special trip to the type locality in an unsuccessful attempt to obtain additional material.

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Department of Zoology, University of Maryland, College Park, Maryland

The Middle Ear of *Holbrookia maculata maculata*, the Northern Earless Lizard

Alvin M. Earle

THE genus *Holbrookia* differs from the other two genera of sand lizards (*Callisaurus* and *Uma*) in the absence of an external ear opening. The purpose of the present investigation is to determine the anatomy of the middle ear of *Holbrookia maculata maculata* Girard. It is hoped that future anatomical research, being done by the present author, on other members of this genus and members of the genera *Callisaurus* and *Uma* will help clarify the taxonomic relationships of these three genera.

In 1898 Versluys described the middle ear of 32 species of lizards; only one of these, *Chameleon vulgaris*, lacks an external tympanic membrane. *Holbrookia* is mentioned but no description of the ear was presented. A cursory account of the middle ear of *Holbrookia maculata* is given by Smith (1938).

Materials and Methods

The specimens of *Holbrookia m. maculata* used in this study, were collected during the summers of 1956 and 1957, three to six miles east of Roggen, Weld County, Colorado. A few fresh skeletons were cleaned with dermestid beetles. The material used for microsections was preserved in Bouin's picroformol fixing fluid, while other specimens were fixed in formalin and later transferred to alcohol.

Heads of specimens were doubly imbedded in celloidin and paraffin according to the method of Dubois (1942). Serial sections were cut at fifteen microns and stained in Mallory's triple stain. Section drawings were made with a microprojection apparatus and various aspects of the ear region were reconstructed following Pusey's (1939) method of reconstruction.

One skeleton was cleared and stained with alizarin red solution (Davis and Gore, 1936). Other specimens were dissected under a dissecting microscope.

In the following account of the muscles of

Holbrookia the terminology used is that of Edgeworth (1935).

Results

Muscles of the ear region.—The superficial musculature of the ear region of *Holbrookia* is represented by the anterior and posterior portions of the depressor mandibulae. The depressor mandibulae posterior is a large triangular muscle having its point of insertion at the articular of the lower jaw. From this point the fibers extend vertically and posteriorly to reach their origin from the dorsal surface of the neck. A small posterior slip of the depressor mandibulae inserts on the fascia of the undersurface of the lower jaw. The constrictor colli is a band-like muscle extending transversely across the throat. It is superficial to the depressor mandibulae and inserts dorsally on the fascia on the dorsal surface of the neck.

The depressor mandibulae anterior is an anterior offshoot of the main portion of the depressor mandibulae. Its posterior fibers arise with the depressor mandibulae posterior. The most anterior fibers of the depressor mandibulae anterior arise from the dorsal portion of the quadrate flange. Fibers posterior to these arise from the squamosal and posterolateral process of the parietal. In *Holbrookia* this muscle is well developed and dorsoventrally lengthened. Its anterior edge runs along the laterally projecting flange of the quadrate and it completely covers the tympanic membrane.

Removal of the depressor mandibulae of *Holbrookia* exposes the tympanic membrane. Posteriorly the tympanum is bounded by the capiti-cleido-episternalis. This muscle extends from the posterior part of the skull and inserts on the sternum.

The capiti-dorso-clavicularis is located immediately posterior to the capiti-cleido-episternalis and inserts on the pectoral girdle. These two muscles extent from their origins along the dorsal surface of the head and neck to converge near their insertions.

The laxator tympani muscle, described in only six species of the gekkonids which were studied by Versluys (1898) and subsequently described by Willard (1915) in *Anolis*, was not found in *Holbrookia*. In the geckos and *Anolis* it extends from the connective tissue covering the processus paroticus of the lateral semicircular canal to the tympanic ligament.

Versluys (1898) also described an elastic tendon, present in most lizards, that may extend from the extracolumella to the processus paroticus. Rice (1920) described this tendon in *Eumeces* as extending from the processus paroticus to the pars superior of the insertion plate and down the insertion plate to the pars inferior. In *Calotes versicolor* a muscle arises from the pars superior of the insertion plate and inserts at the crista parotica. No connection, either ligamentary or muscular, comparable to these structures appears in *Holbrookia* between the distal end of the extracolumella and the skull. *The tympanic cavity.* The tympanic cavity of *Holbrookia* is well developed and has both an anterior and posterior recess. It is similar to the type of cavity found in lizards that perceive air-born sounds. However, laterally it does not approach the skin. Ventrally the tympanic cavity narrows to form the Eustachian tube, which is in wide communication with the posterior roof of the pharynx as described by Smith (1938).

The quadrate and tympanic membrane.—The quadrate of *Holbrookia* articulates above with the squamosal, supratemporal, and crista parotica. It extends ventrally and slightly anteriorly to articulate with the articular. The concavity of the auditory cup or conch is present on the postero-lateral surface of the quadrate and as indicated by Smith (1938) is well developed (Fig. 1). A large, laterally projecting flange is present on the anterior edge of the quadrate.

The tympanic membrane of *Holbrookia* is attached anteriorly to the posterior surface of the quadrate. Posteriorly it is attached to connective tissue beneath the anterior edge of the capiti-cleido-episternalis.

The columella auris.—The columella auris of *Holbrookia* extends laterally and slightly anteriorly from the fenestra ovalis of the otic capsule to articulate with the posterior surface of the quadrate, conforming to the observations of Smith (1938).

The footplate of the columella auris is nearly circular and fills the opening of the fenestra ovalis (Fig. 2); however, it is slightly movable in the dissected specimens. It is completely ossified except for its peripheral areas.

The stalk of the columella auris projects from the footplate and is completely ossified. Relatively thick and almost circular in cross section, it extends about three-fourths of the distance across the cavity of the middle ear and is continuous with the cartilaginous extracolumella.

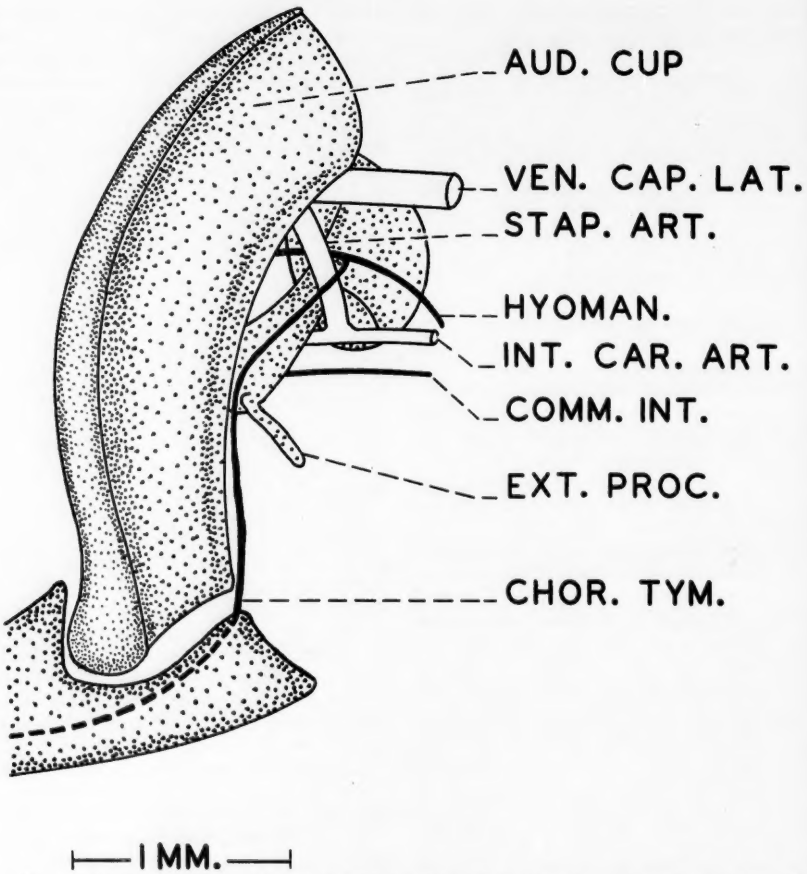

Fig. 1. Schematic reconstruction of the relationships of the blood vessels and nerves to the left columella auris. AUD. CUP., auditory cup of the quadrate; CERAT., ceratohyal; CHOR. TYM., chorda tympani; COL. AUR., columella auris; COMM. INT., ramus communicantes internus; EU. TUBE, Eustachian tube; EXT. PROC., process of the extracolumella; HYOMAN., hyomandibular branch of the facial nerve; INT. CAR. ART., internal carotid artery; LAT. SEM. CAN., lateral semicircular canal; QUAD., quadrate; STAP. ART., stapedial artery; VEN. CAP. LAT., vena capitis lateralis.

The extracolumella is swollen into a knob slightly larger posterior to the main axis of the columella auris. Its distal antero-lateral end articulates firmly with the quadrate.

The crista parotica of *Holbrookia* appears as a thickened cartilaginous ridge on the ventro-lateral surface of the lateral semicircular canal. It projects posteriorly and ventrally to terminate in the processus paroticus described by Versluys (1898), Goodrich (1915), Rice (1920), and others.

A band of connective tissue may persist in some adult lizards between the processus paroticus and the columella auris representing an embryonic dorsal process of the columella auris. This band was not observed in the *H. m. maculata* studied.

A small process, arising from the postero-ventral surface of the extracolumella, projects slightly laterally and ventrally and its distal end is imbedded in the tympanic membrane (Fig. 1). In the alizarin stained specimen this process is stained red, and in section appears to be calcified cartilage. In sections of very young individuals the distal end of this process contacts the tip of the ceratohyal.

The nerves associated with the middle ear.—The nerves traversing the middle ear region of *Holbrookia* follow the same general pattern described for lizards by Goodrich (1915) and de Beer (1937).

The facial nerve of *Holbrookia* leaves the cranial cavity by means of the facial foramen in the prootic bone at the anterior portion of the auditory capsule. The geniculate ganglion is prominent and lies just outside the foramen. The palatine ramus runs anteriorly from this point and the main hyomandibular branch of the facial nerve extends posteriorly. As it enters the region of the tympanic cavity it proceeds posteriorly on the medial side of the cavity ventral to a large vein, the vena capitis lateralis (Fig. 2). It then passes dorsolaterally over the columella auris and posteriorly ramifies to innervate the muscles of the neck region.

The chorda tympani arises from the hyomandibular above the fenestra ovalis immediately posterior to the stalk of the columella auris. It runs in a latero-anterior direction above the stalk of the columella. As previously mentioned, the cartilaginous extracolumella is expanded into a knob and also bears a small process that connects with the vestigial tympanum. The anterior distal end of the knob of the extracolumella articulates with the posterior surface of the quadrate. A small portion of the posterior surface of the knob extends free, posterior to the quadrate. In passing over the extracolumella, the chorda tympani passes above the tympanic process and then over the freely projecting posterior surface of the knob, posterior to the articulation of the anterior portion of the knob with the quadrate. After crossing the extracolumella the chorda tympani proceeds

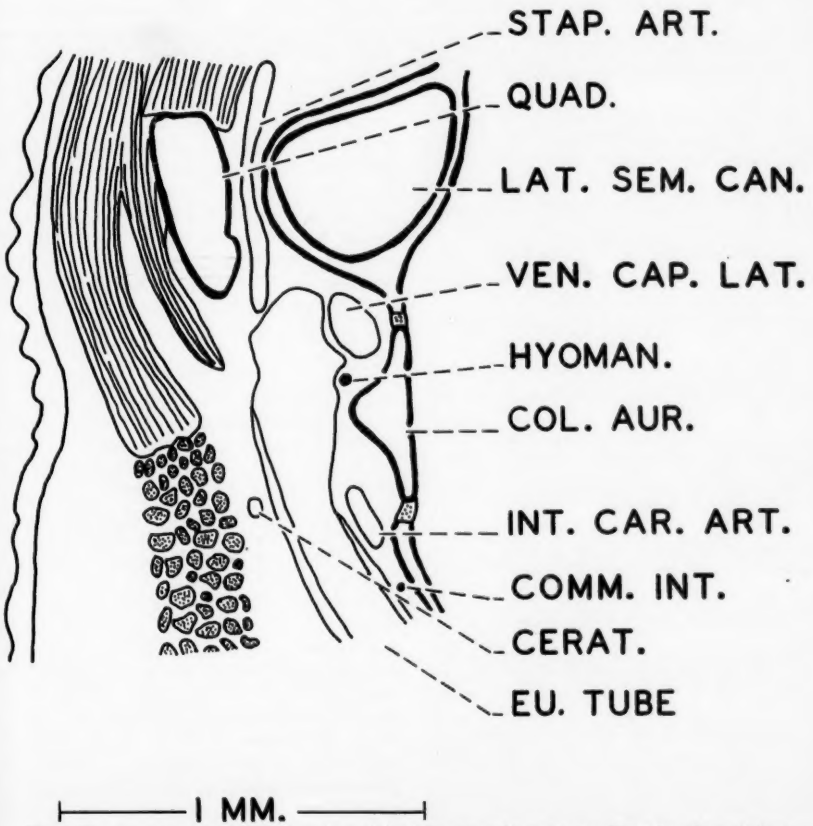

Fig. 2. Transverse section of the footplate of the left columella auris. See Fig. 1 for abbreviations.

down the posterior surface of the quadrate, turns medially, and penetrates the articular through the Meckelian fossa (Fig. 1). In its path through the middle ear cavity the chorda tympani always remains dorsal to the columella auris until it passes ventrally over the freely projecting portion of the extracolumella.

The glossopharyngeal nerve emerges in a normal manner from the apertura lateralis of the recessus scalae tympani and pierces the membrani tympani secondaria which is stretched across this opening. This secondary tympanic membrane does not appear to be strongly developed. Presumably this is correlated with the degeneration of the ear (Brock, 1940).

A small communicating ramus between the glossopharyngeal nerve and the hyomandibular is observed in *Holbrookia*. This ramus, the ramus communicantes externus of Willard (1915), contacts the hyomandibular branch of the facial nerve behind the columella auris. It then runs dorsally out of the region of the tympanic cavity. Willard traced this ramus in *Anolis* and finds that after leaving the tympanic cavity it proceeds anteriorly to form the lachrymal plexus posterior to the eye.

Another connecting ramus, medial to the tympanic cavity, passes under the columella auris forming a communication between the glossopharyngeal nerve and the facial nerve. Willard (1915) calls this nerve the ramus communicantes internus (Fig. 1).

The vena capitis lateralis and the internal carotid artery.—The vena capitis lateralis or internal jugular vein of *Holbrookia* arises from a fusion of veins and sinuses in the posterior region of the orbit. It proceeds posteriorly receiving several tributaries and in the region of the ear assumes a position medial to the quadrate and ventral to the lateral semicircular canal (Fig. 2).

Immediately anterior to the tympanic cavity the vena capitis lateralis receives another vessel coming back from the lower jaw. The vena capitis lateralis enters the anterior tympanic recess at the dorsal surface of the recess and projects from its dorsal wall. Anterior to the columella auris this large vein bends medially to follow the dorsal median wall of the tympanic cavity. It passes over the columella auris and, as mentioned, is dorsal to the hyomandibular ramus of the facial nerve (Fig. 1). Posteriorly the vena capitis lateralis passes out of the posterior recess of the tympanic cavity on its dorsal surface. It then passes down the neck, dorsal to the vagus nerve and the pharynx.

The internal carotid artery runs anteriorly through the neck, ventral to the vagus nerve and dorsal to the pharynx. In the region of the tympanic cavity the internal carotid artery assumes a position lateral to the otic capsule, medial to the tympanic cavity and ventral to the columella auris (Fig. 2). The internal carotid passes ventral to the columella auris and proceeds anteriorly immediately to the hyomandibular branch of the facial nerve.

Anteriorly the internal carotid enters the cranial cavity to supply the brain after a small anterior branch arises from it.

The stapedial artery is larger than the internal carotid and arises from this vessel near the posterior region of the footplate of the columella auris. It passes dorsally and laterally across the tympanic cavity in a diagonal direction (Fig. 2). On its upward course the stapedial artery bends slightly posteriorly and passes over the stalk of the columella auris (Fig. 1). The stapedial artery is closely applied to the posterior surface of the columella auris and passes between it and the chorda tympani. This large artery then passes out of the roof of the tympanic cavity to continue anteriorly between the quadrate and the lateral semicircular canal.

The paths of the vena capitis lateralis, the stapedial artery and internal carotid artery do not appear to differ from those of the same vessels described by Goodrich (1915) for the Lacertilia in general.

Discussion

A conspicuous development of the depressor mandibulae anterior, similar to that observed in *Holbrookia*, has been described by Norris and Lowe (1951) for the "earless" *Phrynosoma m'calli*. They believe that this development is an adaptation to burrowing movements and downward tilting of the head. Smith (1938) has discussed the position and extent of this muscle and points out the general tendency of this muscle to appear enlarged and well developed in lizards lacking an external tympanum. The depressor mandibulae anterior also tends to migrate forward to cover the lateral surface of the quadrate and consequently the tympanum in these forms. In genera such as *Anolis* (Willard, 1915) and *Eumeces* (Edgeworth, 1935) that possess an external tympanum, the depressor mandibulae occurs as a continuous sheet and is not divided into anterior and posterior

segments. In still other lizards such as *Calotes versicolor* (Smith, 1938) and *Varanus* (Edgeworth, 1935) an external tympanum is present, but the depressor mandibulae is poorly developed.

The absence of processes of the columella auris of the *Holbrookia* agrees with Smith's (1938) contention that degeneration of the ear and loss of processes appear to be correlated. He points out that in *Phrynosoma cornutum* the tympanum is thickened and both dorsal and ventral processes are vestigial. *Microsaura* (Engelbrecht, 1951) and *Lophosaura* (Brock, 1940), both members of the Chamaeleontidae, have no tympanic cavity is absent. The extracolumella is devoid of processes in both and is imbedded in the lateral musculature. Brock, however, describes a downward curve of the distal end of the extracolumella and believes this may represent a hyoidean attachment. Bellairs (1950) reports that the columella auris of *Anniella* articulates with the quadrate and shows no processes.

Norris and Lowe (1951) point out that in *Phrynosoma m'calli* the stalk of the columella connects distally with the quadrate bone, and the extracolumella is reduced to a small finger-like projection which is connected to the degenerate tympanum. They do not describe any other processes or connections of the extracolumella. In *Phrynosoma platyrhinos* the extracolumella lies in the external tympanic membrane which, although functional, is partially restricted by the m. depressor mandibulae (Norris and Lowe, 1951). Two processes extend from the extracolumella of *Phrynosoma platyrhinos;* the processus internus which connects the extracolumella to the quadrate, and the processus dorsalis which lies longitudinally in the tympanum over the auditory cup (*ibid.*).

De Beer (1937) has given a complete description of the insertion plate of the extracolumella on the tympanic membrane in *Lacerta*. He calls this a cruciform plate because of its cross-like appearance. The downward projecting arm of the cross is the pars accessorius posterior. During the embryology of *Lacerta* the pars accessorius posterior connects with the ceratohyal by means of a ligament, the pars interhyalis. In *Lacerta* and in *Eumeces* (Rice, 1920) this connection is lost in the adult.

The contact of the extracolumellar process with the ceratohyal in young *Holbrookia* parallels the arrangement in *Lacerta* and it is possible that this process is homologous with the pars accesorius posterior.

Conclusions

The general morphology of the middle ear region of *Holbrookia maculata maculata* corresponds in many respects to that of lizards with a fully developed external tympanum. The major differences are in the extracolumella and the anterior branch of the depressor mandibulae muscle. *Holbrookia* burrows to obtain shelter during periods of inactivity in a manner similar to *Phrynosoma m'calli* as reported by Norris and Lowe (1951). *Holbrookia maculata maculata* and *Phrynosoma m'calli* show a similar enlargement of the anterior branch of the depressor mandibulae and possibly the same selective forces were operative in *H. m. maculata* as those postulated for *P. m'calli.*

Summary

The anterior branch of the depressor mandibulae muscle of *Holbrookia maculata maculata* is strongly developed and covers the tympanic membrane. The curcullaris of *Holbrookia* is represented by the capiticleido-episternalis and the capiti-dorso-clavicularis.

The tympanic cavity of *Holbrookia* is well developed and the Eustachian tubes are in wide communication with the pharynx.

The auditory cup of the quadrate is well developed.

The columella auris extends across the tympanic cavity to articulate with the quadrate. The extracollumella is expanded into a knob and bears a small process which joins the tympanic membrane. No other processes or connections are present in the adult.

The relationships of the hyomandibular branch of the facial nerve and the chorda tympani are similar to those observed in the Lacertilia in general. The chorda tympani passes anteriorly over the posterior distal end of the extracolumella, posterior to its articulation with the quadrate. The glossopharyngeal nerve emerges from the apertura lateralis of the recessus scalae tympani.

The vena capitis lateralis, internal carotid artery, and stapedial artery follow the typical lacertilian pattern. The first two blood vessels pass over the columella auris and the last passes under it.

The evolution of "earlessness" in *Holbrookia* may be linked to selective forces involving its burrowing habits.

The author wishes to express his appreci-

ation to Dr. T. Paul Maslin for suggestion of this problem and for his guidance and encouragement during this work. The author also wishes to acknowledge Dr. Sam Shushan for his suggestions in the preparation of microscopic sections.

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Department of Biology, Regis College, Denver, Colorado

Growth of the Wood Frog, *Rana sylvatica*[1]

Edward D. Bellis

A study of the wood frog, *Rana sylvatica,* was made in the Lake Itasca region of northern Minnesota during the summers of 1954, 1955, and 1956. The frogs were marked and several were recaptured one or more times. It is the purpose of this paper to present data on growth and to discuss these data in the light of previous studies.

The research was done in a peat bog extending northward and eastward from Lake Itasca, the source of the Mississippi River. An area, 120 yards on a side, was marked off in the form of a grid of 100 quadrats with reference stakes placed at twelve yard intervals. An almost pure stand of tamarack covers the northern half of the study area; calla lilies form a lush covering of the viscous, mucky substrate surrounding and separating the tamarack hummocks. The drier southern half is shaded primarily by black spruces, although several other species of trees occur. A dense growth of alders form an understory and the ground is covered by many species of acidophilous herbs, especially heaths. Many mucky, shallow depressions, sometimes filled with water, formed when the trees are uprooted by winds, are scattered throughout the area.

Methods

Wood frogs were captured and marked during July, August, and September of 1954; June, July, and August of 1955; and June and July of 1956. Individuals were marked by toe clipping, and the number, sex, capture site, and body and tibial lengths recorded. The body length (tip of the snout to the vent) was taken with a millimeter rule placed dorsally, the frog being slightly appressed.

Of 1377 frogs handled during the three

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summers, 446 were captured two or more times. Not all of these, however, were used in the determination of growth rates: data derived from captures made in successive or alternate summers were not used, thus any variance between seasons was not obliterated by the combining of data. Data on growth between capture dates of individuals were divided into three categories: males, females, and juveniles. The sex of frogs less than 37 mm. in body length could not be determined with accuracy, although many males measuring 36 mm. and less possessed the swollen thumb used for differentiating the sexes. Under each category the frogs were grouped by size classes of two millimeters, size being indicated as the body length when the initial capture was made. A few larger frogs were omitted because too few observations on these categories were available.

The rate of growth in each case was determined through the division of the change in length by the number of days. A total of 335 rates was determined. The mean length of time between successive captures was 17.3 days.

Results

The results are given in the table and figure.

In the Lake Itasca region larvae metamorphose in July. Body length at metamorphosis is 17–20 mm. The young, recently metamorphosed frogs evidently inhabited the margins of the breeding ponds for several days before they emigrated to the bogs where many of them set up home ranges. Several young were captured as they invaded the study area and some were taken again during the same summer.

The smallest individual captured on the study area measured 21 mm. Nine measuring 22 mm. and many measuring 23, 24, 25, and 26 mm. were taken during the early days of the invasion. Presumably all of these had grown since the time of emergence. Initial growth rates of the invaders were high but decreased in late summer when the 28, 29, and 30 mm. lengths were reached. These sizes predominated in the juvenile population in August and September (Bellis, 1957), coincident with a general lowering of temperature. As the 31–32 mm. stage was at-

Table 1.—Mean Growth Rates of 335 Wood Frogs (*Rana sylvatica*)

	Body length (mm.)	Number of cases	Range (mm./day)	Mean growth (mm./day)	Standard error
Juveniles	21–22	2	.15–.40	.279	.129
	23–24	8	.05–.30	.155	.030
	25–26	11	−.13–.43	.151	.039
	27–28	16	−.06–.43	.135	.033
	29–30	11	.00–.28	.072	.022
	31–32	6	.10–.19	.132	.011
	33–34	9	.08–.32	.186	.026
	35–36	14	.00–.64	.194	.050
Males	37–38	11	.00–.19	.120	.016
	39–40	12	.05–.16	.106	.010
	41–42	37	−.14–.63	.069	.017
	43–44	25	−.14–.29	.041	.017
	45–46	15	−.14–.13	−.031	.020
	47–48	4	−.05–.06	.003	.019
Females	37–38	12	.00–.25	.159	.019
	39–40	8	.00–.29	.112	.034
	41–42	14	−.10–.15	.076	.021
	43–44	27	−.11–.22	.086	.017
	45–46	37	−.09–.29	.077	.011
	47–48	29	−.13–.22	.031	.014
	49–50	7	−.14–.06	.004	.023
	51–52	9	−.28–.20	.009	.045
	53–54	11	−.30–.14	−.005	.038

Fig. 1. Mean growth rates of wood frogs in relation to body lengths. Open rectangles indicate unsexed juveniles; stippled rectangles, females; black rectangles, males. Each rectangle above or below the horizontal line represents one standard error.

tained, the rate increased significantly and showed a progressive increase until the 35–36 mm. length was reached.

Larger animals of both sexes decreased in growth rate consistently, females reaching a larger average size because of a slower decline.

A negative rate of —.031 mm. per day recorded for the 45–46 mm. males was probably the result of inaccuracies in measurement; however, as eight of these 15 frogs showed no change and five a decrease, it is indicative that growth had essentially ceased at this size. Four males measuring 47–48 mm. showed an average rate of only .003 mm. per day. A few larger males were taken during the three summers; the largest was 50 mm. long.

Apparently most females either ceased growth or grew very little after reaching 49 or 50 mm. in length. The 53–54 mm. females showed a negative rate of —.005 mm. per day for 11 individuals. The largest female was 60 mm. long.

The gonads of wood frogs captured in a nearby bog were examined and the size at attainment of sexual maturity determined. Through the plotting of size frequency histograms and the comparison of size peaks (Bellis, 1957) it was determined that females of the Lake Itasca region normally reach sexual maturity two years after emergence and breed the following spring or three years after the eggs from which they developed were laid; for males both of these periods appear to be a year shorter. The evidence indicates that both sexes have nearly stopped growing, at least in body length, by the time they reach sexual maturity.

Discussion

The rate of growth varied greatly between size classes. In general, the smaller frogs grew more rapidly than the larger ones, the growth of the latter being greatly reduced as sexual maturity was attained. All growth studies cited in the bibliography give similar results from the marking of various salientians of the United States.

Growth rates of recently metamorphosed juveniles were initially high but as the season progressed and as the activity periods of the frogs became attenuated due to low environmental temperatures the rates showed significant decreases. Thus, frogs of the 29–30 mm. size group grew, on the average, only .072 mm. per day. Many frogs reach this size by late August or early September. At this time frogs are not active at all during the

coolest days, and, even when the environmental temperature rises above the activity threshold, feeding reactions may be slowed by low temperatures. Also, during this period, less insect and spider food is available. Larger juveniles have a more rapid growth rate, but most of this growth takes place during June and July of the second season, when temperatures are higher, the frogs more active, and more food is available.

Hibernation effects an interruption in the growth of many cold-blooded vertebrates. Low temperatures before and just after hibernation further alter the growth rates and it is only during the warm days of June and July that any size group is able to take fullest advantage of its inherent ability to grow. The effects of low temperatures can best be seen in the smaller individuals because their high growth rate permits good comparisons between seasons; older individuals are affected to a lesser degree. A graduated sigmoid curve is obtained when the body length is plotted against age. Seasonal variation has been reported by Ryan (1953), who showed that the rate in young leopard frogs (*Rana pipiens*) is less during the colder months of the active season, such as May and September, than during the months of June, July, and August. Blair (1953), in a study on *Bufo valliceps* in Texas, found that the spring rate is higher than the winter one. Martof (1956) showed that the rate in the green frog (*Rana clamitans*) is positively correlated with the mean monthly air temperature, being higher during June, July, and August.

It is not known whether juvenile males and females differ in growth rates, but at the 37–38 mm. stage, and, as the animals are becoming mature, females grow faster than males and consequently are larger by the time they breed. Ryan (1953) found that the rate of growth of male green frogs is generally slower than that of the females. Martof (1956) detected no major differences between growth of male and female green frogs but found that females grow somewhat faster in the larger size groups. In the amphibian group as a whole, mature females are generally larger than the males.

Wood frogs show clinal size differences throughout much of their range; northern populations are composed of shorter, stockier individuals. In view of this, no generalizations can be made about the maximum size attained outside the Minnesota region. At Lake Itasca, however, it appears that 50 mm. is the maximum body length for males and 60 mm. for females, although very few individuals reach these sizes. Most males probably terminate growth at 46 mm. and most females at 50 mm. It is not known whether growth is determinate among frogs. Raney and Ingram (1941) suggest that bullfrogs and green frogs attain a certain length and then cease growth altogether. This may be the case among wood frogs; there is no evidence to the contrary. However, perhaps older individuals grow slightly every summer, thus exhibiting an asymptotic type of growth.

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Department of Zoology and Entomology, Pennsylvania State University, University Park, Pennsylvania.

Calcified Hyoid and Mesopodial Elements of Plethodontid Salamanders

THOMAS M. UZZELL, JR.

IN most salamanders of the family Plethodontidae the carpals and tarsals are cartilaginous, and among the hyoid elements only the second basibranchial is ossified. Three Middle American genera, *Thorius, Parvimolge,* and *Lineatriton,* have been reported to have mesopodials or hyoid elements other than the second basibranchial osseous or calcified (Cope, 1869; Rabb, 1955). These ossifications or calcifications have been used both to delimit taxa and to indicate relationships. Conflicting reports concerning the presence of these ossified or calcified elements suggested their evaluation as systematic characters.

METHODS

Radiographs of series of *Thorius pulmonaris, Parvimolge townsendi, Lineatriton lineolus* and various other plethodontids were made with a beryllium-window x-ray machine, using the techniques described by Miller (1957). The radiographs were examined for x-ray opaque areas in the hyoid and mesopodials. Opaque hyoid elements were easily detected. Most of the available specimens of *Lineatriton* and *Parvimolge* were not preserved in positions convenient for x-ray study of the limbs, and the number of x-ray opaque mesopodials in them could not be determined accurately. The series of *Thorius,* however, was preserved with the trunk straight and the limbs at right angles to the body, and in these the number of opaque mesopodials could be counted.

In order to verify the radiographic determinations of ossified or calcified mesopodials, three of the x-rayed specimens of *Thorius pulmonaris* were cleared and stained with alizarin red S. One, a large adult female (26.9 mm.), had the maximum number of x-ray opaque mesopodials observed in *Thorius;* a second female (24.5 mm.) had an intermediate number; a third female (23.4 mm.) was the largest that had no opaque mesopodials. In each of these the number of elements that stained with alizarin agrees with the number that were x-ray opaque. It is felt, therefore, that the use of x-rays to determine the presence or absence of ossifications or calcifications is justified, and that the results obtained are consistent with those that would be obtained by other methods.

The mesopodials of *Thorius* and *Parvimolge* have been considered to be bone (Cope, *op. cit.*; Taylor, 1944; Rabb, *op. cit.*). The alizarin-staining hyoid elements in *Parvimolge* and *Lineatriton* have been considered either bone or cartilage (Rabb, *ibid.*). In order to determine the nature of these elements, some of each were sectioned and examined microscopically. The terminology used by Tanner (1952) for hyoid elements and throat muscles is followed.

A second ceratobranchial from a specimen of *Lineatriton lineolus* with the maximum number of x-ray opaque hyoid elements was decalcified, sectioned, and stained with hematoxylin and eosin. In cross section the element is largely cartilage. No bone can be distinguished; if it is present, it exists only as an extremely thin layer at the periphery of the element. Another second ceratobranchial from the same animal was stained with alizarin, cleared, and sectioned. The alizarin is distributed throughout each section, and not restricted to the peripheral area.

Mesopodials of *Thorius pulmonaris* stained with hematoxylin and eosin appear to be entirely cartilaginous. No bone can be detected, and if it is present, it is restricted to the periphery of the elements. Alizarin-stained material indicates that calcification is present throughout the elements.

In view of the large amount of calcified cartilage present in the elements that were sectioned, and the possibility that bone is completely absent, they are referred to as calcified cartilage in further discussion. The mesopodials of *Parvimolge* and *Lineatriton* and the hyoid elements of *Parvimolge* have not been sectioned. In alizarin-stained material, these elements have a granular appearance which frequently distinguishes calcified cartilage from bone; they are therefore also considered to be calcified cartilage.

GENUS *Thorius* COPE

Sixteen large males and 18 large females of *Thorius pulmonaris* were examined. The males, 21.0 to 24.5 mm. from the tip of the snout to the posterior angle of the vent, have

enlarged testes; in five, the testes are bilobate, indicating by analogy with *Desmognathus* at least three reproductive cycles (Humphrey, 1922). None of the females contains enlarged eggs, but their lengths (20.0 to 26.9 mm.) suggest that many of them are mature.

No calcification in the hyoid was detected in any of the specimens of *Thorius*, nor has any been reported.

Calcifications in the mesopodials occur in 12 of the 34 adults. There is a correlation between body length and number of calcifications (Table 1). In the females the maximum number of calcifications occurs at larger sizes than in males. Females also have calcification over a wider size range. The ontogenetic increase in total number of calcifications is thus more gradual than in males.

Table 1. Snout-Vent Lengths in mm. and Total Number of Calcified Mesopodial Elements in Adults of *Thorius pulmonaris*

Males		Females	
Snout-vent length	Total number of calcified mesopodials	Snout-vent length	Total number of calcified mesopodials
21.0–21.8 (n = 8)	0	20.0–23.4 (n = 11)	0
22.3	1	23.8	11
22.6	28	24.4	13
22.8	0	24.5	9
23.2	5	25.6	0
23.3	28	25.9	26
23.5	0	26.5	28
24.3	28	26.9	28
24.5	28		

Hilton (1946:7) has illustrated the elements in the tarsus of *Thorius pennatulus*. He showed seven cartilaginous elements: tibiale, fused intermedium and fibulare, a single centrale, and four tarsalia. The outermost tarsale illustrated articulates only with the fifth toe.

The largest number of calcified tarsal elements in *T. pulmonaris*, based on x-rays and on cleared and stained material, is eight: tibiale, fibulare, intermedium, a single centrale, and four tarsalia (Fig. 1, right). This series occurs in 12 ankles of seven individuals. The intermedium and fibulare appear united into a single element, since there seems to be no movement of one independent of the other. There are, nevertheless, two distinct centers of calcification. Proximally, this double element articulates almost entirely with the fibula. The centrale and outermost tarsale are also possibly united, although again two calcification centers are distinct. The outermost tarsale, in contrast to the condition illustrated by Hilton in *Thorius pennatulus*, supports both the fourth and fifth digits.

From the specimens having incomplete sets of calcifications, an attempt was made to determine the ontogenetic sequence of calcification. In all feet with incomplete sets of calcifications, the outermost tarsale is calcified; in one foot it is the only calcification. When two elements are calcified, they are the outer tarsale with the intermedium, the

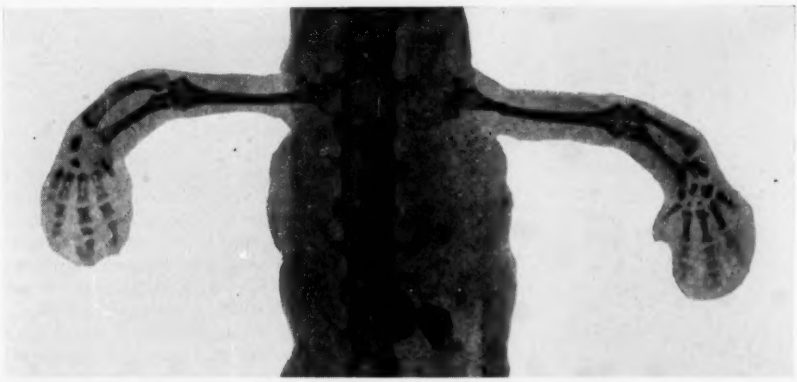

Fig. 1. Hind limbs of *Thorius pulmonaris*, showing asymmetry of digits and in number of tarsal calcifications, the left foot normal, the right foot probably regenerated.

fibulare, or the centrale. The only combination of three elements includes the outer tarsale, the intermedium, and the fibulare.

Elements calcifying earlier in ontogeny should be calcified more frequently in incomplete sets. In nine ankles with incomplete sets of calcifications, the following frequencies occur: outer tarsale, 9; intermedium and fibulare, 6 each; centrale, 5; tibiale and second tarsale, 2 each. The first and third tarsalia are calcified only in ankles with complete sets. The sequence based on frequencies is thus consistent with that based on combinations.

Hilton (1946) figured the carpals of *Thorius pennatulus*, showing seven cartilaginous elements: radiale, fused intermedium and ulnare, a single centrale, and four carpalia. In x-rays and stained material of *T. pulmonaris* I have examined, there are as a maximum seven centers of calcification and six separate elements (Fig. 2); the large centrale articulates with the fourth digit, and there are but three carpalia. Because it articulates with the fourth digit, the centrale probably includes a fourth carpale. In animals with incomplete sets of calcifications, the intermedium and ulnare have separate centers of calcification; they are fused in those that have complete sets. In the x-rays, the intermedium and ulnare were counted as a single element. In the cleared and alizarin-stained individual with an incomplete set of calcifications, the intermedium, but not the ulnare, is calcified. The centrale is calcified in this individual, and shows only a single center of calcification.

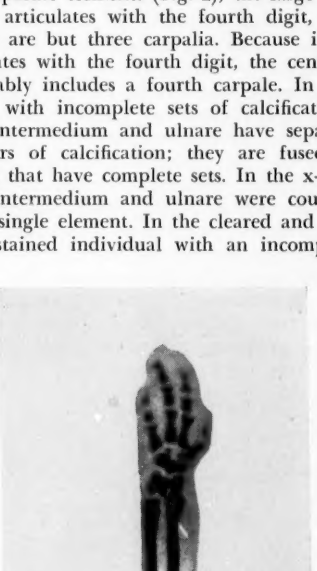

Fig. 2. Front limb of *Thorius pulmonaris*, showing calcified carpal elements.

In wrists that have only one calcified element, calcification occurs in the centrale three times, in the fused ulnare and intermedium twice. In wrists with two calcified elements, both of these units are calcified. In the remaining specimens with incomplete sets, all elements but the third carpale are calcified. The frequencies of calcification are: centrale, 9; fused intermedium and ulnare, 8; radiale, carpale one, and carpale two, 3 each. The apparent order of calcification thus is: centrale, intermedium, ulnare, radiale and carpalia one and two, and carpale three.

Two males (22.6 and 24.3 mm.) and one female (26.5 mm.) have complete sets of calcifications in three of four feet. In the larger male, the fourth foot is missing. The smaller male has only two calcifications in the right hind foot (Fig. 1), and the female has none in the left fore foot. The lower number of calcified mesopodials in a single foot suggests loss and regeneration of a limb, especially since the smaller male has but four well developed toes on the right hind foot. In Table 1, these three specimens have been listed as having a full complement of calcified mesopodials.

Genus *Parvimolge* Taylor

All three of the species that have been assigned to this genus have been examined: 18 specimens of *P. townsendi*, one of *P. praecellens*, and 4 of *P. richardi*.

The series of *P. townsendi* consists of nine large males, eight large females, and a juvenile. The males (17–23 mm.) have enlarged premaxillary teeth, swollen nasolabial protuberances, and prominent mental glands, and are evidently mature; the largest has bilobate testes. Some of the females, which range from 18 to 24 mm., contain enlarged ovarian eggs. In Table 2, the relation of body length to calcification is given for each sex.

Calcification in the hyoid of *P. townsendi* was noted by Rabb (*op. cit.*), who reported ossifications or calcifications in the second ceratobranchials of an alizarin-stained specimen. Calcification in the second ceratobranchial occurs throughout the element. Calcification in the epibranchial occurs just posterior to the articulation with the second ceratobranchial, in an area about as long as its diameter.

Because of difficulties in x-raying the limbs, accurate counts of the calcified elements are not available. Rabb (*ibid.*) found eight carpals, with the ulnare and centrale [*sic*] partly fused. He also found at least seven, probably nine, tarsals. An additional stained specimen has five separate units in one wrist, and six in the other, with eight centers of calcification: radiale, fused ulnare and intermedium, a single centrale, and four carpalia, the outermost of which is fused with the centrale in one foot. The first digit is in contact with the first and second carpalia. There are eight tarsals: tibiale, intermedium, fibulare, a single centrale, and four tarsalia, the outermost of which articulates with the two outer digits. The first digit is in contact with the first and second tarsalia. In this specimen only the tibiale and first tarsale are uncalcified.

I have x-rayed the holotype of *Parvimolge praecellens*, an apparently immature female about 35 mm. (Rabb, *ibid.*). It has neither mesopodial nor hyoid calcifications.

One male, two females, and a juvenile of the Costa Rican *Parvimolge richardi* were x-rayed. The male (25 mm.) has enlarged naso-labial protuberances and a swollen, papillate vent, indicating that it is sexually mature; the testes are unilobate. One of the females (24 mm.) has enlarged ovarian eggs and a greatly enlarged oviduct, while the other (23 mm.) has a greatly enlarged oviduct but no enlarged ovarian eggs; both are apparently mature. None of specimens shows any evidence of hyoid or mesopodial calcification.

The immature specimen of *P. praecellens* does not provide satisfactory data on the presence or absence of hyoid and mesopodial calcifications in this species. Adults of *richardi* lack the calcifications, and the species may not be congeneric with *P. townsendi* on other evidence. For these reasons, following references to *Parvimolge* apply only to the type species, *P. townsendi*.

Genus *Lineatriton* Tanner

Sixteen specimens of the single species, *L. lineolus*, were examined. One had been cleared and stained with alizarin; the remainder were x-rayed. All seven males have enlarged premaxillary teeth, and the testes of two are bilobate. The six females do not contain enlarged eggs, but are in the same size range as the males and probably mature. Snout-vent length and extent of calcification for the 13 mature individuals are given

Table 2. Relation of Snout-Vent Length (mm.) to Calcification in Adult *Parvimolge townsendi*

Calcification	Males	Females
None	17, 20	
Second ceratobranchials		18, 19
Second ceratobranchials, some mesopodials	21, 22, 22, 23, 23, 23	21, 22, 22, 24
Second ceratobranchials, some mesopodials, epibranchials	20	22, 24

Table 3. Relation of Snout-Vent Length (mm.) to Calcification in Adult *Lineatriton lineolus*

Calcification	Males	Females
None	34.0, 35.3	31.4, 33.0, 35.2
Second ceratobranchials	34.5, 37.4, 42.1	38.2, 40.2
Five hyoid elements, some mesopodials	38.2, 41.1	40.8

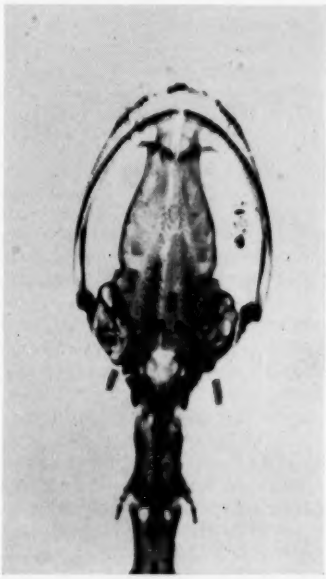

Fig. 3. Head of *Lineatriton lineolus*, showing full complement (5) of hyoid calcifications.

in Table 3. The three juveniles (21.7–30.8 mm.) examined have no hyoid or mesopodial calcifications.

Calcification in the second ceratobranchials was reported by Rabb (*ibid.*). Of the eight specimens with calcified hyoid elements (Table 3), five have only the second ceratobranchials calcified, while the remaining three also have the first basibranchial and epibranchials partly calcified (Fig. 3).

Calcification in the second ceratobranchial occurs throughout the length of the element. The basibranchial has a center of calcification located posteriorly, anterior to the articulation of the second ceratobranchials and apparently adjacent to or posterior to the articulation of the first. In x-rays, the opaque area is one to two times as long as the diameter, and of a diameter suggesting that the basibranchial is calcified throughout the cross-sectional area. The calcification in the epibranchials varies from half to a quarter of the length of the second ceratobranchials. It is located just posterior to the articulation with the second ceratobranchial, and apparently occupies the entire cross section of the epibranchial.

Difficulties were encountered in determining the number of calcified mesopodial elements (Table 3), but they seem to vary from one to five in the wrist, and from one to three in the ankle. Hilton (1946) figured nine tarsals and eight carpals for *Lineatriton*.

Calcification in the mesopodials apparently occurs later than in the hyoid elements, since only those individuals with five calcified hyoid elements have any calcified mesopodials.

Other Genera

Several genera of plethodontid salamanders in addition to *Parvimolge*, *Lineatriton*, and *Thorius* were examined. Alizarin-stainable and x-ray opaque areas were found in various hyoid elements of several species of *Plethodon*, *Desmognathus*, and *Manculus*. Of 16 adult *Plethodon glutinosus*, 8 had some calcification in the first basibranchial. A bony area in the first basibranchial of several species of *Plethodon* has been reported (Wiedersheim, 1877; Piatt, 1935; Hilton, 1945a), and bony areas in the first ceratobranchials of *Plethodon glutinosus* were noted by Wiedersheim and by Hilton. Three of 11 adult *Desmognathus wrighti* and 2 of 6 adult *Desmognathus fuscus* had some calcification in the first basibranchial. Of 15 adult *Manculus quadridigitatus*, 8 had some calcification in the first basibranchial; calcification in the first ceratobranchials occurred in 2, and in the second ceratobranchials, in 4.

Wiedersheim (1877:498) reported calcified epibranchials in various, undesignated species of *Spelerpes*. I have examined specimens of all the genera Wiedersheim would have included in *Spelerpes*, but I cannot find calcified epibranchials except in *Lineatriton*, *Parvimolge*, and in gilled forms of the eastern North American free-tongued genera.

In the six specimens of *Batrachoseps* examined, the second basibranchial is not ossified or calcified, contrary to the condition figured by Cope (1889, pl. 35, fig. 4). Piatt (*op. cit.*: 236) described the second basibranchial of *Batrachoseps* as much reduced, but Hilton (1945b, c) reported it as entirely absent in several forms of *Batrachoseps attenuatus* and in *B. wrighti*.

None of the specimens of genera examined in this study other than *Lineatriton*, *Parvimolge*, and *Thorius* has ossified or calcified mesopodials, although they have been reported exceptionally in *Plethodon glutinosus* by Dunn (1926), and may have been observed in *Desmognathus fuscus* by Steiner (1921, fig. 2).

Function

The mesopodial calcifications of *Thorius*, *Parvimolge*, and *Lineatriton* and the hyoid calcifications of various plethodontid genera may have some selective advantage in terms of function. A comparison of the orders of calcification of the carpals and tarsals of *Thorius pulmonaris* reveals some interesting similarities. The first element to calcify is the outermost distal element, the fourth tarsale or, in the wrist, the centrale. The second element in the wrist is the fused intermedium and ulnare, with perhaps the intermedium the earlier; in the ankle the intermedium and fibulare apparently calcify at the same time. The third element in the ankle is the centrale, corresponding to a part of the wrist already calcified. Thus, in both wrist and ankle the outer mesopodials seem to calcify before the inner.

Schaeffer (1941:419) suggested that in the hind limb of caudate amphibians the weight is transmitted from the femur to the tibia, and then to the fibula for distribution to the foot. It seems likely that the order of calcification of the elements in the wrist and ankle is in part related to forces acting through them in locomotion. That the intermedium and ulnare fuse in the wrist and

the intermedium and fibulare are very closely joined in the ankle may also reflect the action of these forces. Schaeffer (*ibid.:* 400) has offered a similar interpretation to account for apparently earlier ossification of the outer tarsal elements of *Archegosaurus.*

Detailed information about the sequence of mesopodial calcification in *Parvimolge* and *Lineatriton* is not available, although the outer sides of the wrist and ankle seem to calcify earlier. The relation of bony to cartilaginous mesopodial elements in several other species of salamanders suggests that this is the usual situation. Illustrations of *Taricha granulosa* and *Salamandra* (Hilton, 1948) show a cartilaginous series along the inner margin of the wrist and ankle, the outer elements being bony. Stokely and Holle (1954) reported that the prepollex and radiale in the wrist and prehallux and tibiale in the ankle of ambystomatid salamanders are usually more weakly ossified than the other mesopodials.

Rabb (*op. cit.:* 8) suggested that several characters of *Parvimolge townsendi* could be interpreted as the result of paedomorphosis. Reasoning further along this line, the development of calcified mesopodials in *Thorius, Parvimolge,* and *Lineatriton* may compensate for the paedomorphic and presumably weak condition of the adult foot of these genera; the absence of calcified mesopodials in other weak-limbed plethodontid genera may reflect different kinds of locomotion in those forms.

Accounts of hyoid action in protruding the tongue of free-tongued or adetoglossal (from *adetos*-free or unfettered, plus *glossos*-tongue) plethodontids have been given by Wiedersheim (1875) for *Hydromantes italicus* and by Smith (1920) for *Eurycea bislineata.* The muscles involved are the *m. subarcualis rectus I* and the *m. geniohyoideus lateralis.* The *m. geniohyoideus lateralis* has its origin on the mandible, and inserts on the posterior end of the ceratohyal. This muscle and the articulation of the ceratohyal with the skull serve to fix the anterior end of the ceratohyal. The *m. subarcualis rectus I* provides the main propulsive force in projecting the tongue. It has its origin on the anterior ventral end of the ceratohyal; its fibers run posteriorly, ventral to the ceratohyal and the ceratobranchials, to the epibranchial, around which they form a cup-like sheath. This sheath is composed of two layers, the fibers of which run diagonally to the long axis of the epibranchial, and spiral around it in opposite directions. The sheath joins the epibranchial only at the latter's posterior end. When the fibers of the *m. subarcualis rectus I* contract, the sheath is both shortened and pulled forward; pressure applied to the posterior end of the epibranchial pushes the entire tongue mechanism forward. The force operates through the epibranchial, the ceratobranchials, and the basibranchial. To judge by the arrangement of the *m. geniohyoideus lateralis* and the *m. subarcualis rectus I,* the protrusion of the tongue in attached-tongued or detoglossal (from *detos*-bound or fettered, plus *glossos*) plethodontids involves similar muscle actions.

The elements that move the tongue vary in length and robustness. In the detoglossal genera, the first ceratobranchials are relatively thick compared to the second, and the epibranchials are equal to or shorter than the first ceratobranchials except in *Batrachoseps* in which they are relatively long. The hyobranchial apparatus in the eastern North American adetoglossal genera, including *Eurycea,* is similar: the first ceratobranchials are relatively robust, and the epibranchials are as long as to twice as long as the first ceratobranchials. The remaining adetoglossal genera, including *Hydromantes,* have the first ceratobranchials much reduced in comparison to the second, and the epibranchials very long, usually three to four times as long as the first ceratobranchials. The distance to which the tongue can be projected probably depends on the length and action of these elements.

Among the genera of plethodontids examined, calcified or ossified elements in the tongue-moving series were found in *Desmognathus, Plethodon, Manculus, Parvimolge,* and *Lineatriton.* In *Desmognathus* and *Plethodon,* both detoglossal genera, the most frequent and presumably earliest calcification occurs in the first basibranchial. The first ceratobranchial in *Plethodon* calcifies also, but less frequently and therefore probably later. In *Manculus,* an eastern North American adetoglossal genus, the order of calcification suggested by frequencies is first basibranchial, second ceratobranchials, first ceratobranchials. In *Parvimolge* and *Lineatriton,* Middle American adetoglossal genera, the apparent sequence is second ceratobranchials, epibranchials, and finally, in *Lineatriton,* the first basibranchial. *Manculus,* therefore, has an order of calcification of tongue-moving hyoid elements more similar to that in the detoglossal genera. This agrees

with the similarity in the proportions of the hyoid elements.

The pressure applied at the posterior end of the epibranchials is probably transmitted to the first basibranchial largely through the more robust pair of ceratobranchials. When these are the first pair, the first basibranchial calcifies relatively early, prior to the first ceratobranchials; when these are the second pair, the first basibranchial calcifies relatively late, after the second ceratobranchials. The second ceratobranchials in *Manculus* calcify before the first pair, but after the first basibranchial; this suggests that these elements share the transmission of forces to the first basibranchial. Nevertheless, if the proportions of the tongue-moving elements of the hyoid and the sequence of calcification of these elements are related to the action of these elements in projecting the tongue, the action of the tongue in *Manculus*, though intermediate, probably resembles the tongue action of the detoglossal genera more than it resembles that of the Middle American genera.

The different sequences of calcification of hyoid elements among plethodontid genera may indicate relatively great differences in the action of the tongue. The absence of calcification in most of the genera suggests slight differences in tongue action between those genera that develop hyoid calcifications and closely related taxa that do not.

Phylogenetic Considerations

The use of calcifications in the hyoid and mesopodial elements as systematic characters requires consideration of their frequency. Series of *Thorius pulmonaris, Lineatriton lineolus,* and *Parvimolge townsendi* show a large measure of variation in the calcification of these elements. In adults of these three species, the order of constancy in calcification is: second ceratobranchials of *Parvimolge townsendi* (88% of specimens examined), mesopodials of *P. townsendi* (76%), second ceratobranchials of *L. lineolus* (66%), mesopodials of *T. pulmonaris* (47%), mesopodials, first basibranchial, and epibranchials of *L. lineolus* (25%), and epibranchials of *P. townsendi* (18%). Juveniles of these species have no calcifications in these elements. In view of this variation, the use of these calcifications as "presence or absence" characters is unwarranted. They may, however, be useful in determining relationships and in delimiting groups.

The plethodontid salamanders fall into two fairly well-marked groups: those with the tongue attached to the floor of the mouth by a strip of tissue running from the anterior margin to the central pedicel, and those in which the central pedicel forms the only attachment of the tongue; the adetoglossal condition is specialized. Two of the detoglossal genera, *Desmognathus* and *Leurognathus,* with generally aquatic tendencies, are morphologically isolated from the other, more terrestrial, detoglossal genera. The adetoglossal genera form two or three subgroups. The less specialized eastern North American genera have an aquatic larval stage; they retain the *m. omohyoideus* and the second basibranchial; the first ceratobranchials are relatively robust compared to the second, and the epibranchials are generally no more than twice as long as the first ceratobranchials (Tanner, 1952; 653). The numerous remaining genera, including *Parvimolge, Lineatriton,* and *Thorius,* have, as far as is known, no aquatic larval stage.

Of the three genera in which mesopodial calcifications occur, *Thorius* has been placed in a separate family (Cope, 1869) or in a separate subfamily of the Plethodontidae (Smith and Taylor, 1948). To consider the calcified mesopodials of *Thorius* a subfamilial character is unwarranted in view of their occurrence in *Parvimolge* and *Lineatriton.* The incomplete roofing of the skull of *Thorius,* another skeletal feature that has been adduced to support its separation from other plethodontid genera, resembles the condition in *Batrachoseps.* Nevertheless, the musculature and skeletal features noted by Tanner (*op. cit.:* 655), the pseudocoelous vertebrae (Soler, 1950), and the position of the subocular groove, isolate *Thorius* from other Middle American genera.

The subocular groove intersecting the lip in *Thorius* calls to mind the subocular groove and notch of *Eurycea* and *Manculus,* and suggests a separate, early derivation of *Thorius* from the *Eurycea-Manculus* line. On the other hand, the position of the subocular groove and the condition of the skull bones and the feet may be paedomorphic characters. If so, it becomes easier to include *Thorius* with the other specialized adetoglossal genera. Muscular similarities have been noted by Tanner (*op. cit.*). The long epibranchials and weak first ceratobranchials (Tanner, *op. cit.:* pl. 74, fig. G), and the absence of the second basibranchial also ally *Thorius* with the more specialized adetoglossal genera. Little is known about the life history of

Thorius, but the locality at which I have collected the genus, near Acultzingo, Veracruz, Mexico, did not offer a likely habitat for aquatic larvae. Although the position of *Thorius* remains unclear, this genus is probably more closely related to the geographically close genera of Middle America than it is to the eastern North American genera.

Parvimolge and *Lineatriton* have been considered closely related genera (Tanner, *op. cit.*). Rabb (*op. cit.*) noted that the distinctive calcifications in the second ceratobranchials of these two genera support their relationship. The calcification in the epibranchials and the sequence of calcification are additional evidence.

The mesopodials of primitive families of salamanders are cartilaginous or consist of a block of cartilage encased by bone. In contrast, the calcified mesopodials of *Thorius*, *Parvimolge*, and *Lineatriton*, while cartilaginous, are calcified throughout; bone is apparently absent. Since these genera belong to a specialized section of the family, it seems likely that the calcified mesopodials of these genera arose within the Plethodontidae. The mesopodial calcifications of *Parvimolge* and *Lineatriton* probably reflect closeness of relationship. The calcification of the mesopodials in *Thorius*, however, may be a convergence with *Parvimolge* and *Lineatriton*.

Material Examined

The species examined represent various groups of plethodontid genera. They include forms related to those with calcifications in the hyoid and mesopodials as well as a variety of body sizes and foot types. The following detoglossal forms were examined: *Batrachoseps attenuatus* (x-rayed: 4; cleared and stained with alizarin: 2); *Desmognathus fuscus* (0, 6); *D. wrighti* (10, 1); *Plethodon glutinosus* (12, 4). Adetoglossal forms examined were: *Manculus quadridigitatus* (14, 1); *Hydromantes brunus* (3, 0); *H. genei* (2, 0); *H. platycephalus* (3, 0); *H. shastae* (1, 0); *Bolitoglossa rufescens* (7, 3); *B. striatula* (1, 0); *Chiropterotriton chondrostega* (6, 2); *C. dimidiatus* (3, 1); *C. priscus* (3, 1); *Lineatriton lineolus* (15, 1); *Magnadigita cuchumatana* (3, 0); *Oedipina uniformis* (4, 0); *Parvimolge praecellens* (1, 0); *P. richardi* (4, 0); *P. townsendi* (16, 2); *Pseudoeurycea cephalica* (12, 1); *P. galeanae* (3, 0); *P. scandens* (7, 0); *Thorius pulmonaris* (34, 3). The three cleared stained specimens of *Thorius pulmonaris* were from the series x-rayed.

Acknowledgments.—Ernest E. Williams of the Museum of Comparative Zoology, Harvard College, allowed me to examine specimens of *Parvimolge townsendi* and the holotype of *Parvimolge praecellens*; William E. Duellman of the Museum of Natural History, University of Kansas, provided me with specimens of *P. richardi*. To both I wish to express my thanks for the use of this material. Charles F. Walker and George B. Rabb have kindly read the manuscript and offered valuable suggestions. To them also I wish to express my thanks. The illustrations for this paper were made by means of an electron beam photographic printer; I am very grateful to Rainer Zangerl of the Chicago Natural History Museum, who very kindly gave time and energy to providing these for me.

Summary

The frequency of calcification of hyoid and mesopodial elements in adults of *Parvimolge townsendi*, *Lineatriton lineolus*, and *Thorius pulmonaris* varies; juveniles of all three lack calcifications. The use of these calcifications as "presence or absence" characters is therefore unwarranted, although they may be used to indicate relationships.

Calcification was observed in the mesopodials of *Thorius pulmonaris*, *Lineatriton lineolus*, and *Parvimolge townsendi*. In *T. pulmonaris*, the outer tarsals and carpals calcify before the inner ones. The sequence of calcification may reflect the transmission of forces from the lower limb to the hand or foot during locomotion.

Calcified or ossified hyoid elements were observed in several species of *Plethodon*, *Desmognathus*, *Manculus*, *Parvimolge*, and *Lineatriton*. In *Plethodon* and *Desmognathus*, the first basibranchial is the earliest element to calcify. In *Parvimolge* and *Lineatriton*, other elements calcify prior to the first basibranchial. The different sequences are correlated with differences in tongue attachment, relative robustness of first and second ceratobranchials, and length of epibranchials; all are probably related to tongue action. *Manculus*, although intermediate, probably resembles *Plethodon* and *Desmognathus* more than *Parvimolge* and *Lineatriton* in tongue action.

The mesopodial and hyoid elements of *Parvimolge*, *Lineatriton*, and *Thorius* apparently differ from those of non-plethodontid salamanders in developing calcified cartilage rather than bone. Since these genera belong in a specialized section of the family,

the calcifications probably arose within the family.

The systematic position of *Thorius* is uncertain. The genus has some unique characteristics, some which suggest relationships with the eastern North American adetoglossal genera, and some which suggest relationships with the Middle American adetoglossal genera. Placing *Thorius* in a separate subfamily seems unwarranted. Interpretation of some of the characters of *Thorius* as paedomorphic makes it reasonable to group *Thorius* with the Middle American adetoglossal genera.

The calcified mesopodial and hyoid elements of *Parvimolge* and *Lineatriton* probably reflect closeness of relationship. The calcified mesopodials of *Thorius* may be a convergence with those genera.

The absence of calcifications in the mesopodials and hyoid elements of adult *Parvimolge richardi* suggests that *richardi* is not congeneric with the type of the genus, *P. townsendi*.

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Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

The Mechanics of Sound Production in North American *Bufo*

Wayne H. McAlister

THE study of vocalization and of the response to auditory stimuli in anuran amphibians has progressed from the early incidental field observations of Courtis (1907) and Miller (1909) and the experiments of Yerkes (1905) to the present state of precise field documentation (Noble and Noble, 1923; A. P. Blair, 1942; Cory and Manion, 1955; Littlejohn, 1958) and objective laboratory analysis (Potter, 1950; W. F. Blair, 1957, 1958b; Crenshaw and Blair, 1959; Littlejohn and Main, 1959). Considerable work has been done on the physiological aspect of sound production and hearing (Dempster, 1930; Witschi, *et. al.*, 1953a, b; Witschi and van Bergeijk, 1954; van Bergeijk, 1957; van Bergeijk and Witschi, 1957; Kleerekoper and Sibabin, 1959). In brief, the investigations

have indicated that the majority of anurans can produce sounds, that they are capable of hearing and recognizing sounds within a frequency range compatible with their vocalizing abilities, and that vocalization and audition play a significant role in anuran biology at both the intra- and interspecific levels.

The present investigation was undertaken to determine the structures that are involved in sound production in North American *Bufo* and how these structures function during sound emission. This study encompasses most of the species of *Bufo* occurring in the United States. The classification and species grouping of Blair (1958a) have been followed.

Methods

The primary vocal structures (vocal cords and larynx) were removed from fresh and preserved material, stained with toluidin blue, and examined under low magnification. Investigation of the secondary vocal structures involved the vocal pouch, mouth slits, and gular muscles. They following method was used to estimate the dimensions and shape of the inflated vocal pouch: a) the toad was killed by pricking the brain; b) the nostrils and mouth were sealed with a coating of latex and quick-drying varnish; c) a thin glass tube was inserted into the pyloric end of the stomach, pushed through the esophagus and into the buccal cavity; d) the lungs were tied off near their insertions into the larynx; e) a special apparatus (described and illustrated by McAlister, 1959) was attached to the exposed end of the abdominal tube, and volume and pressure values were determined as the pouch was inflated with air. In some instances the inflated pouch was coated externally with latex. The solidified latex mold was later filled with plaster of Paris and the resultant cast was used to determine pouch shape.

Mating calls were recorded in the field with a PT6J Magnecorder and a Magnemite (Amplifier Corporation) tape recorders at a tape speed of 15 inches/second. The recordings were analyzed with a sound spectrograph (Kay Electric Company). The principle of operation of the spectrograph is presented by Fletcher (1953) and its use in the study of anuran calls is detailed by Blair and Pettus (1954), Blair (1955), and Zweifel (1959). A sample call of each species was viewed on a cathode ray oscilloscope. Following the procedure of Frings and Frings (1956) carbonyl iron (General Aniline and Film Corporation; Grade E) orientation patterns were utilized to study the fine structure of the recorded calls.

Terminology

In the subsequent discussion of sound production several physical and biophysical terms are used. Some of these terms are elaborated below not because they are uncommon to the non-physicist, but rather because they are often misused.

If an elastic particle is displaced from its position of equilibrium and then released and allowed to vibrate freely, the frequency of vibration will be its *natural frequency*. The natural frequency is not a constant for it varies inversely with the damping resistance of the system. The time interval required for the completion of one particle vibration is the *vibration period*. When a particle is vibrating at its natural frequency, the time interval required for one vibration is the *natural period*. The maximum displacement of a vibrating particle from its equilibrium position is called its *amplitude*. Generally as the frequency increases the amplitude of vibration decreases, and the energy involved is consequently decreased.

When a vibrating system with a low damping resistance is acted upon by a periodic force, the periodicity of which approximates the natural period of the system, high amplitude *resonant vibrations* will occur in the system. A small force may thus *amplify* the vibrations of the system. The natural period of the system will increase as the damping resistance increases. The *resonant period* will not change, however, and it will be equivalent to the natural period only when there is little damping resistance. Therefore the *resonant frequency* may not be equivalent to the natural frequency if the damping resistance is appreciable.

The sound produced by a high-grade tuning fork is termed a *pure tone* because it is composed largely of one frequency. Sounds produced by the vocal cords are *complex tones* because they are composed of many frequencies emitted simultaneously. The lowest frequency (the *fundamental frequency*) is accompanied by arithmetically related higher frequencies or *harmonics*. It is the characteristics of these harmonics which are differentially affected by the resonators in the vocal system to produce a sound of a characteristic *quality*.

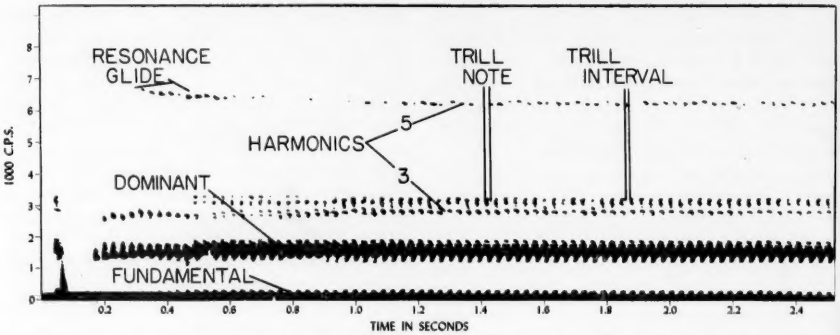

Fig. 1. Sound spectrogram of a portion of the mating call of *Bufo valliceps*. Call begins at the left.

Pitch is that apparent predominant frequency of a sound as heard by the ear. The pitch is determined by the fundamental frequency, the intensity, and the harmonic structure of the sound (Colby, 1934). Thus a low fundamental or a high intensity in a low frequency harmonic (or both) can cause a lowered pitch. The pitch as perceived by the ear may not be a linear function of the frequency if the ear is differentially sensitive to various frequencies.

The following terms are more subjective than the foregoing, but their usage is fairly well standardized. It was proposed at the Paris Colloquium on Acoustics of Orthoptera (1954) that a sound produced by a single cycle of operation of the producing mechanism be termed a *syllable*. In the present paper the term "*trill note*" is used to designate that burst of sound which is produced by a single vibration of the vocal cords (Fig. 1) and it is therefore synonymous with the term 'syllable." The *trill rate* (trills/sec) is equivalent to the fundamental frequency of the sound phonated. The *trill interval* is that silent interval between two successive trill notes. The *dominant frequency* is that harmonic, or series of adjacent harmonics, in which the greatest amplitude of vibration occurs. A *call* is any regular burst of trill notes. A toad call may be considered terminated when there is a noticeable interruption of trill note production (*i.e.*, when the trill interval is inordinately expanded). A toad call is considered to be *trilled* if the trill interval is of sufficient duration to allow the individual trill notes to be distinguishable to the human ear; in an untrilled call the trill notes are not audibly separable. With proper laboratory manipulation all recorded calls were found to be composed of trill notes and thus the trilled-untrilled distinction is not a basic one.

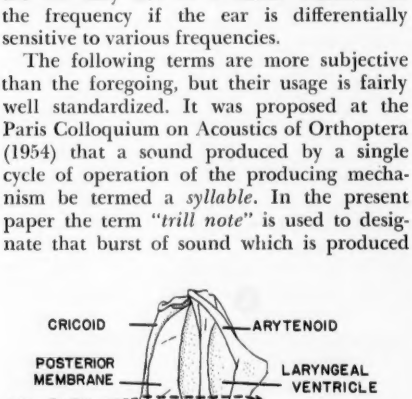

Fig. 2. A. Semidiagrammatic sagittal section through the larynx of *Bufo valliceps*. B. Diagrammatic frontal section of the primary vocal apparatus of *Bufo speciosus*.

Anatomical Investigation

Primary Vocal Structures. The vocal cords and larynxes of 65 adult and seven juvenile toads were examined. The interior of the *Bufo* larynx is unlike that described for ranids (Holmes, 1930; Noble, 1931). There is a depression in the laryngeal wall (*laryngeal ventricle;* Stanley, 1932) immediately posterior to the glottis. Behind the ventricle the vocal cords occur, followed by a second pair of membranes that resemble the cords in conformation (Fig. 2). The vocal cord arises from the arytenoid (anterior) portion of the larynx and is angled forward. The base of the cord is thickened, as is the outer

margin bordering the free edge. In some species the central portion of the cord is cartilaginous and this region is here termed the *midrib*. Although the cord is thickened parallel to its free edge, the edge itself is thin and posteriorly recurved (Fig. 2B). There is no evidence of the thickened, grooved edge seen by Noble (1931) and Holmes (1930) in ranids.

The pair of posterior membranes arises from the cricoid (posterior) portion of the larynx. These membranes lack a midrib, and the region near the free edge is not thickened. The free edge is occasionally recurved near its lateral margin, but medially it is not folded.

The relation of the various laryngeal structures to each other and the direction of air flow through the larynx during sound emission indicate that the membranes serve as an air baffle. That is, as air enters the larynx from the lungs, it must travel up the inclined surface of the posterior membranes. The free edges of the membranes are directly in line with the recurved edges of the vocal cords. The recurved lateral region of the membranes may serve to funnel the air stream medially, directly to the vocal cord edges. The cord edges would then intercept the air flow "edge-first" and vibrations should be quickly initiated. Possibly the thin edge of the cord oscillates laterally while the cord proper vibrates anterioposteriorly. It is doubtful that the posterior membranes vibrate enough to be termed sound producers.

The most striking result of this examination of the *Bufo* larynx is the similarity of structure in all species studied. Despite dissimilar calls, the larynxes show little interspecific divergence.

The larynx of *B. alvarius* is of especial interest because Blair and Pettus (1954) commented on the vestigial call of this toad. Examination of three males revealed a large larynx with well developed vocal cords. Any loss of call capability apparently must be caused by failure of some other portion of the vocal mechanism. *B. boreas* is a toad that does not emit a mating call even though the primary vocal structures appear well formed. Blair (1956b), in an account of the mating calls of two interspecific toad hybrids, *B. americanus* × *woodhousei* and *B. woodhousei* × *valliceps*, suggested that intermediate laryngeal structures might account for some of the characteristics of the hybrid calls. Five *B. woodhousei* × *valliceps* hybrids as well as both parental species were available for the present study. The hybrid larynx showed no unique features, and the parental species exhibited no consistent interspecific differences. It is concluded that the intermediate nature of the hybrid call is not principally caused by the nature of the primary vocal structures.

Secondary vocal structures.—That diverticulum of the buccal cavity lining which is inflated during sound emission and which occurs in most adult male anurans has been termed the vocal sac or vocal pouch. The anatomy of this structure has been considered by Noble (1931), Liu (1935), Inger (1956; 1958), and Inger and Greenberg (1956). The description of the muscular and tissue components of the *Scaphiopus* vocal sac given by McAlister (1959) might serve as well for the vocal pouch of *Bufo*. Following the system of Liu (1935), the pouches of the toads studied are categorized in Table 1.

In general only two shapes are assumed by the inflated pouch: spherical or sausage-like (Fig. 3). The former may vary from a nearly true sphere (*B. punctatus*) to an ovate shape with extensions along the insertions of the forelegs (*B. valliceps*). The sausage pouch is best exemplified by the extreme condition of *B. cognatus* and *B. speciosus*, in which the pouch curves upward in front of the rostrum. The pouch of *B. quercicus* is termed an abbreviate sausage because it is relatively neither as elongate nor as reflected as in *B. cognatus* and *B. speciosus*. The shape of the inflated pouch of a specimen of *B. woodhousei* × *valliceps* is about intermediate between that of the parental forms (Fig. 3).

The vocal pouches of nine species of toads and one hybrid were compared by using the inflation apparatus. The results are presented in Table 2. The pouch of each individual was inflated twice to a pressure of 8 cm. of water, and the volume results were averaged (column 4). The several species are directly comparable only in column 3. Actual pouch volume varies directly with body size. With the exception of the large pouch of *B. cognatus*, the relative volume of the vocal sac does not vary markedly in the several species studied, although those forms with a sausage-like sac have a slightly greater relative volume. In some instances a pouch was inflated to a constant pressure before and after removal of the gular skin. Results indicate that the gular skin of smaller individuals stretches less easily than that of larger conspecific individuals. There is also an indication that when a minimum body size is achieved in ontogeny (about 61 mm. in *B. speciosus*) the

TABLE 1. CHARACTERISTICS OF THE INFLATED VOCAL POUCHES OF TOADS (*Bufo*)

Species	Wright & Wright (1949)	Liu (1935)	Direct Observation	Other
B. valliceps	round, subgular	MSI[1]	spherical	—
B. marinus	—	MSI	—	—
B. quercicus	sausage	MSE	abbreviate sausage	—
B. speciosus	sausage	MSE	sausage	—
B. cognatus	sausage	MSI	sausage	—
B. terrestris	—	MSI	spherical	—
B. americanus	—	MSI	—	—
B. hemiophrys	sausage	MSI	—	spherical (oral) Blair
B. houstonensis	—	—	spherical	"
B. microscaphus	—	—	—	"
B. woodhousei	—	MSE	—	"
B. fowleri	round, subgular	MSI	spherical	—
B. punctatus	rounded	MSE	spherical	—
B. debilis	round ball	MSE	spherical	—
B. boreas	—	MSI	—	—
B. canorus	—	MSI	—	—
B. alvarius	—	MSI	spherical	MSI & PSI (Inger, 1958)

[1] MSI-median subgular internal; MSE-median subgular external; PSI-paired subgular internal.

pouch abruptly becomes capable of greater expansion.

Dissection of the vocal pouches of 12 species of toads revealed no striking interspecific structural differences. One individual *B. woodhousei* × *valliceps* had a pouch internally divided into two compartments. The specimen was capable of producing a mating call. Blair and Pettus (1954) reported that the vocal pouches of 12 male *B. alvarius* were more or less vestigial. Inger (1958) examined a larger series and came to the same conclusion. The pouch of a single male used in the present study possessed a thick gular skin and a little-modified subhyoid muscle. The left half of the subhyoid was fused to the median gular muscles.

The most variable of the secondary vocal structures appears to be the pair of mouth slits through which air in the buccal cavity enters the vocal pouch. These openings are usually slit-like and are situated in the floor of the mouth near the margin of the tongue. *B. boreas* and *B. alvarius* both have more circular openings set near the corners of the lower jaw. The slits vary in number (one or two) and in size. The slits in the same individual toad may differ in length. During artificial pouch inflation it was observed that the slit-like opening became nearly circular.

In the species studied, at a point along the hyoid just distal to the anterior curvature, there is a short, flattened region. Beyond this flattening the horn continues to the corner of the mouth, tapering and becoming rounded in crossection. Several times a pithed toad which was still exhibiting muscular reflexes raised the hyoid bone and pushed it forward. The flattened portion of the hyoid and the surrounding tissue occluded the mouth slit. This may be the normal mechanism for closing the connection between the buccal and pouch cavities.

CALL ANALYSIS

General.—Before presenting the results of the call analysis several basic assumptions of how the toad vocal mechanism operates should be introduced.

The vocal cords are the primary sound producers in anurans. It is the natural frequency of the cords that determines the fundamental frequency of the sound. The natural frequency of the cords can be altered by changes in their linear density and/or tension (i.e., by modifying the damping resistance). To produce a complex tone the cords must vibrate in a complex manner, since the presence of each harmonic demands that some portion of the cords be oscillating at a cor-

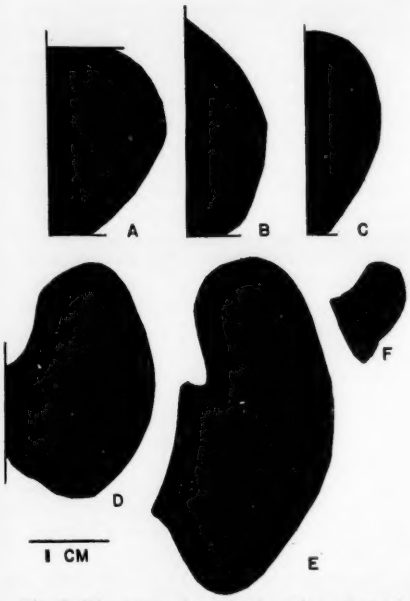

Fig. 3. Diagrammatic sagittal sections through the inflated vocal pouches of adult male toads (*Bufo*). Drawings from plaster casts: *B. valliceps* (C), *B. woodhousei* (A), *B. woodhousei* × *valliceps* (B), and *B. speciosus* (D). Drawings from direct measurements on inflated pouches: *B. cognatus* (E), *B. quercicus* (F).

responding frequency. The cords may also regulate sound intensity (the "registration" function of Stanley, 1932). If the cords stiffly abut in the laryngeal lumen, a greater air pressure is required to burst them apart. The greater energy dosage produces a sound of higher intensity. The functions of the vocal cords are: a) production of sound, b) frequency modulation, c) intensity regulation.

If only the laryngeal structures were involved in producing sound, toad calls would differ only in loudness and frequency. That the calls are highly species-specific is evident. It is the role of the resonant cavities to add amplitude modification to the primary sound. Amplitude modulation is one of the chief factors determing sound quality.

The function of a vibrator-resonator system can best be understood with reference to a model. Figure 4 presents a model that can be compared to the vocal mechanism of a toad. The flask is analagous to the toad larynx and the air source to the air contained in the lungs. A pair of rubber membranes stretched across the flask mouth represents the vocal cords. Three fixed and one variable resonators terminate the system, and these correspond to vocal pouch, mouth cavity, laryngeal ventricle, and other resonators in the toad system.

As the initial complex sound wave traverses the first resonator, those frequency bands nearest the resonant frequency of the res-

Table 2. Results of Inflation Tests on the Vocal Pouches of Toads (*Bufo*)

Species	Snout-Vent L. (mm)	Pouch Vol/ Snt.-Vent Length	Average of Trials 1 & 2 (cc)
B. speciosus	53.2	0.06	3.2
"	55.9	0.12	6.5
"	57.0	0.14	6.5
"	57.3	0.13	7.3
"	60.0	0.10	5.8
"	61.5	0.23	14.3
"	64.6	0.19	12.5
"	67.8	0.26	17.3
B. valliceps	51.0	0.04	1.9
"	83.0	0.21	17.4
B. debilis	46.8	0.06	2.9
B. woodhousei	66.1	0.08	5.4
B. woodhousei × *valliceps*	74.0	0.13	9.4
B. alvarius	145.0	0.18	26.7
B. quercicus	24.0	0.04	0.9
B. houstonensis	54.0	0.08	4.2
B. punctatus	45.3	0.03	1.1
B. cognatus	80.4	0.30	24.2
"	83.2	0.28	22.9

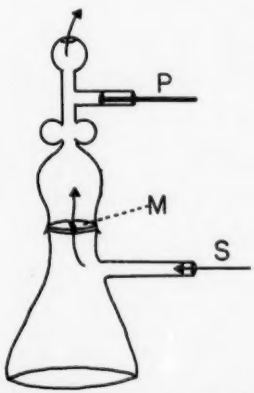

Fig. 4. Physical analogue to the toad vocal mechanism. See text for comparison of physical and biological systems. Abbreviations: P., piston of variable resonator; M, rubber membranes; S, input air source. Arrows indicate direction of air flow.

onator will be amplified. The same phenomenon occurs in the other resonators. Some frequency bands may be unaffected and some may be damped. Movement of the piston in the variable resonator changes its resonating quality. Active pumping of the piston during sound emission can cause *resonance glide*, or a gradual shifting of the amplified bands (Fig. 1). The final sound radiated from this model system is totally unlike the unmodulated noise produced by the vibrator.

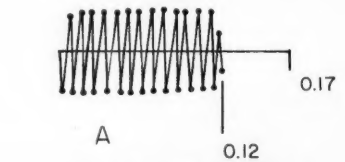

Fig. 5. Drawings from oscilloscope photographs of the mating calls of three species of toads (*Bufo*). Oscillations caused by dominant frequency. A. Single trill note of *B. americanus*. B. Single trill note of *B. speciosus*. C. Section from middle of the call of *B. quercicus*.

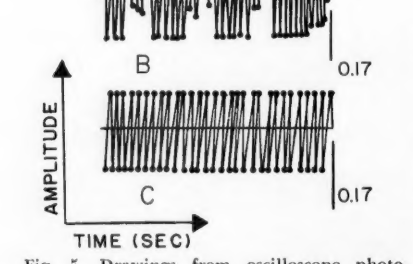

Fig. 6. Correlation of trill rate with body size and temperature in *Bufo valliceps*. Each symbol represents an average value from the analysis of six calls of one individual toad. All toads from a single breeding aggregation.

Trill note production.—The vocal cords impart the trilled characteristic to the call. The cords can function in two ways: a) If the cords stiffly abut in the laryngeal lumen they can completely damp all edge vibrations each time they close during one vibration cycle. Thus the call would consist of a series of sound parcels, the frequency of which is determined by the natural frequency of the cords. b) If the cords fail to abut or are less firmly maintained, a continual air flow and edge vibration could occur. If the cords have a high natural frequency, a whistle might be produced.

Figure 5 is a diagram of the oscillogram pattern of a portion of the recorded mating calls of three species of toads. The trill note structure exemplified by *B. americanus* is most typical for the genus. There is an initial rapid accumulation of energy, a short high-intensity sound pulse, and an abrupt cessation of sound. The trill interval is free of cord movement.

In *B. cognatus* there is a frequency and amplitude fluctuation within each trill note. This fluctuation can be explained by assuming that during the relatively long vibration period the cords flutter and partially interrupt the edge vibrations. This phenomenon is also characteristic of the call of *B. speciosus* and occasionally occurs in several other species of toads.

The call of *B. quercicus* is unique among those examined because it shows no trilled structure except near its beginning and end. The oscillogram indicates continual cord edge oscillation. This is apparently the only toad studied in which the vocal cords function as described in the second of the alternatives mentioned above.

Trill rate.—The number of trills per second is a reflection of the activity of the vocal cords. Several workers have noted the effect of temperature on the trill rate (Bellis, 1957; Blair, 1958a; Zweifel, 1959). The mating calls of 13 marked toads (*B. valliceps*) from a single breeding aggregation were recorded in the field at two air temperatures. The results (Fig. 6) indicate a positive trill rate-temperature correlation, which is in accord with the data of most other investigators.

It is generally conceded that body size and trill rate show an inverse correlation. The above series of *B. valliceps* yielded ambiguous results on this point. Any rela-

tionship that exists may not be a rigid one, for if the species of *Bufo* under consideration are aligned according to size, the large *B. marinus* and *B. alvarius* are found at one size extreme with average corrected trill rates of 9.5 and 67.0 trills/second respectively. Several smaller species have trill rates below that of *B. alvarius* (Table 3).

The studies of Blair (1958a) on toads and of Johnson (1959) on tree frogs indicate that trill rate can vary geographically within a given anuran species. Littlejohn (1959) failed to find significant intraspecific trill rate differences in the calls of *Crinia insignifera* and *C. signifera*.

Dominant frequency.—The dominant "frequency" is usually a frequency band, and often a broad band (Fig. 1), which may vary in frequency as the call progresses. This results from the broad and dynamic tuning characteristic of the resonator responsible for its production. Despite the obvious function of the vocal pouch as a sound resonator, it was not unequivocally demonstrated that the pouch is responsible for the occurrence of the dominant frequency. The specific structure or structures that serve to amplify one frequency band above all others remains undetermined.

An inverse correlation between dominant frequency and body size occurred in the series of 13 *B. valliceps* mentioned above. This relationship is loosely true if the toad species are grouped according to body size and compared with the average dominant frequencies of their mating calls. The call of a *B. woodhousei* × *valliceps* hybrid was unique because it began with a dominant band at 1200–1800 cps, and near the middle of the call a second dominant appeared at 1900–2900 cps. The second, higher band is found in neither of the parental species, and the lower band falls within the dominant range of both parents. Blair (1956b) gives an excellent spectrographic illustration of such a call.

The dominant frequency band has been shown to vary directly with temperature in *Hyla versicolor* (Blair, 1958a) and in *Microhyla* (Blair, 1955). A similar result was obtained in the present study with the calls of 13 *B. valliceps* and eight *B. speciosus*. However the dominant in the calls of a single specimen of *B. terrestris* recorded at 18° and 23°C showed an inverse temperature correlation.

The temperature effect on raising or lowering the dominant frequency band may be caused by an alteration in the operation of the vibrator, the resonator, or both of these. An examination of the carbonyl iron orientation patterns of the calls of 13 *B. valliceps* indicates that it is the vocal cords (the vibrator) that are functionally temperature dependent. When the iron particles are sprinkled onto a strip of recording tape upon which a trill note is recorded, the particles orient themselves over the area of the trill note in a pattern of close-set vertical bars. The number of bars per unit length of tape can be equated to the dominant frequency of the sound phonated. The frequency of the iron particle bars can be changed only by modification of the vibrating mechanism. It was found that the frequency of the bars did vary directly with temperature in the calls of *B. valliceps*.

Duration. The duration of the toad mating call varies from 0.15 seconds in *B. quercicus* to more than a minute in *B. cognatus*. McAlister (1959) concluded that gular skin elasticity was a factor controlling call duration in *Scaphiopus* by limiting vocal pouch expansion. Blair (1956b) showed that hybrid calls had intermediate durations, indicating that call length is polygenically controlled. Michaud (1959) and Zweifel (1959) noted an inverse correlation between call length and

TABLE 3. AVERAGE CORRECTED TRILL RATES OF THE MATING CALLS OF TOADS (*Bufo*)[1]

Species	Average Trill Rate, Blair (1956a) (22°C)	Sonagram Analysis (22°C)
B. marinus	9.5	9.5
B. quercicus	—	—
B. valliceps	33.9	32.0
B. alvarius	—	67.0
B. americanus	35.7	—
B. houstonensis	34.5	37.2
B. terrestris	72.0	77.0
B. microscaphus	—	53.0
B. henniophrys	—	93.5
B. woodhousei	—	165.0
B. fowleri	—	116.0
B. debilis	119.0	125.0
B. punctatus	50.5	60.0
B. cognatus	17.5	16.5
B. speciosus	45.0	35.7
B. woodhousei × *valliceps*	—	60.5
B. woodhousei × *americanus*	58.5	—

[1] Data in the third column adjusted to 22°C by using a positive trill rate-temperature correlation and a factor of one trill note/second/C°.

temperature in *Pseudacris* and *Bombina* respectively.

Air flow mechanics.—The vocal mechanism of toads is unique because it represents an entirely closed system. Students have long puzzled over the means by which an air stream is maintained past the vocal cords. Most workers (Noble, 1931; Liu, 1935; Inger, 1956) concluded that there is a reverse mechanism which periodically pushes air from the vocal pouch into the lungs. It has been suggested that the gular muscles ordinarily used for breathing might provide the impetus for rearward air movement. Another mechanism might involve the elasticity of the wall of the vocal sac. If the sac were maximally expanded during the utterance of a trill note, its force of restitution might send an air parcel posteriorly during the succeeding trill interval. A third alternative is commensurate with the first, except that the mouth slits might be closed and the air exchange would then be between the buccal cavity and lungs rather than involving the vocal pouch.

In the author's opinion the chief criticism of each of the above mechanisms is that serious objections can be proposed against their universal application to all toads. Throughout this study striking interspecific similarity has been discovered in the vocal mechanism. Therefore one would expect the control of air flow to be alike in the several toad species. In accord with this idea a fourth alternative which is universally applicable and in many ways more plausible (at least in the species studied) can be presented—that there is no rearward air flow during call emission. Workers in human vocalization (Stanley and Maxfield, 1933) have emphasized that the net movement of air required to set the vocal cords into vibration is very small. It is therefore conceivable that increase in pouch volume is continual during call emission, or that the air in the pouch and buccal cavities is put under compression as the call progresses. Both phenomena probably occur. Gradual pouch enlargement is visible in some calling toads (*B. speciosus; B. quercicus*), but not in others (*B. valliceps*). The acceptance of the assumption that there is no reverse air flow in *Bufo* makes the vocal mechanism of toads similar to that proposed for *Scaphiopus* (McAlister, 1959). An interesting exception to this air flow scheme is described for *Bombina variegata* (Zweifel, 1959) in which sound production apparently occurs during rearward rather than forward air movement.

Summary and Acknowledgements

This study is concerned with the physical and biophysical aspects of sound production in North American *Bufo*.

The *Bufo* larynx encloses an anterior pair of vocal cords and a posterior pair of membranous flaps. The latter structures probably facilitate phonation by directing the air flow to the vocal cord edges, thus initiating sound-producing oscillations. The larynx shows no striking interspecific variation in the 17 species of toads studied.

The anatomy of the vocal pouch is basically similar in the species examined, although when inflated it assumes one of two different shapes: spherical or sausage-like. The vocal pouches of nine species of toads were artificially inflated and they showed slight interspecific differences in relative volume.

The vocal cords are the primary sound producers in anurans, and they also function in frequency modulation and intensity regulation. The rest of the vocal structures probably serve as amplitude modulators.

A rise in temperature causes an increase in trill rate and a rise in the frequency of the dominant band. It was determined that in *B. valliceps* the vocal cords are the structures which are functionally temperature dependent.

Increase in body size is usually accompanied by a lowered trill rate and dominant frequency, although the correlation is not a rigid one.

There may be a continual forward-directed air flow through the vocal apparatus during sound emission (as opposed to the earlier theory of an intermittent rearward movement).

I am indebted to Dr. W. F. Blair, the University of Texas, who supervised this study and read the manuscript.

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DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF TEXAS, AUSTIN, TEXAS.

Functions of the Brooding Behavior in the Female Red-backed Salamander, *Plethodon cinereus*

RICHARD HIGHTON AND THOMAS SAVAGE

ALMOST all of the literature references to field observations on the eggs and embryos of *Plethodon cinereus* mention an associated brooding female (Bishop, 1941: 206, and others). During 1958, 1959 and 1960, Duvall Jones, Donald Widman and the writers found 117 nests containing advanced embryos in the vicinity of Mountain Lake, Giles County, Virginia. All but six of these were attended by spent females.

We have made observations on brooding females in the laboratory that indicate two advantages that result in positive survival value to the developing embryos that are as-

sociated with the brooding habit. An experiment by Highton showed that the presence of the female increases the proportion of embryos that survive and develop normally, while observations by Savage indicated that the brooding female actively defends her nest against predatory salamanders.

Effect of Female on Development

Seventeen gravid female *Plethodon cinereus* collected May 28, 1960, on Catoctin and South Mountains, Frederick and Washington Counties, Maryland, were injected with mammalian gonadotropic hormone (Gonadogen) four days later by the method of Anderson (1958). The specimens were separated in glass jars containing moistened filter paper and these were placed in a constant temperature incubator at 20° C. Fourteen of the females deposited eggs from June 4 to June 6, but several ate some or all of their eggs before examination. Dissection revealed eggs in the stomachs of seven of eleven specimens that were removed and preserved on June 6. The remaining six females deposited five (3), six (2) and seven eggs and coiled around them in the typical manner of females in nature and were not disturbed. Thirty-four eggs were thus incubated with the parent present, while the females were removed from jars containing the remaining nineteen eggs. The eggs were not disturbed while the female salamander was taken out of the jar.

On June 14, the six females still with their eggs were examined. One that had eaten 3 of 5 eggs was dead; her remaining eggs were decomposing. Two other females were no longer coiled around their eggs and each had consumed one of the original clutch, which consisted of five and six eggs. Both were removed from the jars containing the eggs. Of the three remaining females, one (with seven eggs) had not eaten any, while the other two had eaten two of five and two of six eggs, leaving a total of fourteen embryos remaining with the three brooding parents. All of these developed normally and hatched from August 4 to 11. Thus every embryo that was allowed to remain with a brooding female throughout development and that survived the first ten days hatched.

Only three of nine embryos of the two broods kept with their female parents until June 14 (8–10 days) hatched and one of these died shortly after hatching, on August 10. Of the nineteen eggs separated within two days after deposition, only six, or 32% (in three of the eight broods) hatched (August 2 to 11). Compared with the fourteen that had been incubated by their female parents, these embryos were smaller in size and had much more yolk at hatching. On preservation on August 15, the average total length of the fourteen incubated eggs was 24.0 mm. (range 22–26), while that of the six hatchlings that developed without attending females was 17.4 mm. (range 14–23 mm.). The two whose parents were removed on June 14 were 20 and 22 mm. in total length. In a previous experiment (Highton, 1960), using 476 eggs of *Plethodon cinereus* deposited in the laboratory and immediately separated from the females, only 30% of the embryos survived to hatching.

How does the presence of the brooding female enhance the chances of survival and normal development of the embryos? Noble (1931:413) states that the body of the parent of terrestrial plethodontids provides moisture for the embryos and that her dermal secretions apparently prevent mold from growing on them. He presented no proof, merely observing that some eggs are destroyed by mold when removed from the parent. We have found that mold usually grows only on dead embryos. No mold grew on living eggs or embryos during the course of this experiment, although it grew on the filter paper in the jars. Since this was true of all three groups of embryos, it would seem likely that if present at all, any mold-inhibitor was produced by the embryo. Daniel and Simpson (1954) failed to find evidence of an antibiotic effect in the skin secretion of three aquatic salamanders (*Diemictylus viridescens, Necturus maculosus* and *Ambystoma tigrinum*). The brooding females usually maintained contact with their eggs, perhaps providing the developing embryos with water or other substances not available in the substrate. We have often noted that brooding females collected in the field excrete or secrete a watery liquid from the cloaca in excess of that produced by non-brooders. The chemical role of these cloacal and integumentary secretions in development is not known.

We suspect that oophagy is related to the unnatural conditions in the laboratory. The number of eggs in natural nests averages somewhat less than the number of ovarian eggs (9.1) reported by Blanchard (1928:159), so that it is possible that this practice also occurs in nature. Wood and Clarke (1955) re-

ported a case in *Desmognathus fuscus* and Noble (1931:413) mentioned egg-eating by cryptobranchid salamanders.

The three groups of embryos incubated in the laboratory were not selected at random, but were chosen because of the behavior of the female: if she abandoned the nest or ate some of her eggs, she was removed, but if she brooded normally she was allowed to remain. It is conceivable that the variation in the development of the embryos could be due to other factors than the presence of the female. For example, females may have abandoned or eaten only those embryos that were already dead. Experimental bias of this type is unlikely, however, and could not account for the differences in size of the three groups of surviving offspring.

Observations of Brooding Behavior

It is usually assumed that the brooding female defends its nest, although little supporting evidence has thus far been obtained. Gordon (1952:683) observed brooding female *Aneides aeneus* make aggressive lunges and bites toward objects inserted into nest crevices. However, other individuals of *Aneides aeneus* did not elicit such responses and no observations on potential predators were made.

In order to observe the behavior of female *P. cinereus* a shelter of moist paper toweling was constructed in the bottom of gallon jars turned on their sides to facilitate observation. On May 5, 1960, five gravid females from near Cooksville, Howard County, Maryland, were injected with gonadotropic hormone and placed in separate containers. One female escaped from the jar and three others ate their eggs before any observations could be made, but the fifth deposited seven eggs on May 11 and remained with them. They hung in a bunch from the roof by a thin thread of jelly. The jar was kept in the dark at 23° C and observations were made under reduced red or white light.

When food (fruit flies and spring tails) was introduced into the jar, the female would occasionally leave the shelter and forage. Usually, however, she sat under the eggs, and often pressed the anterior part of her body along their surface. Several times the egg mass was observed to spin when she moved away, suggesting that it has been twisted by her movements. Two females from the same locality were separately introduced into the container. On a number of occasions when one approached the nest, the brooding female vigorously attacked and bit the intruder. The latter always retreated without defending itself. The brooding female always kept her head between the eggs and the intruder.

One female was left in the jar with the brooding female for thirteen days. On the last day it was noted that two of the seven embryos had disappeared. The foreign female was immediately dissected and yolk material was found in its stomach. All five remaining embryos hatched between July 2 and 7. The hatchlings were observed sitting on their mother's head and body. Newly hatched young in nature have also been found in this position.

Throughout the observations three aspects of behavior were prominent: the eggs appeared to be the focal point of the female's behavior, intruders were chased with vicious bites and the female characteristically took a position under the eggs with her head and anterior portion of the body touching them.

Summary

An experiment to determine the effect of female *P. cinereus* on the development of embryos has shown that her presence promoted growth and utilization of yolk material as well as survival. Some females ate their eggs soon after deposition in the laboratory.

Embryos separated from the female parent had less than a third the survival rate (to hatching) of those incubated by the female. Incubated hatchlings averaged 6.6 mm. longer than non-incubated ones.

A single female brooding in the laboratory actively defended her eggs against other salamanders. Nevertheless, an introduced female devoured some embryos.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF MARYLAND, COLLEGE PARK, MARYLAND

Relationship of Two Whiptail Lizards (Genus *Cnemidophorus*) in Western Mexico

RICHARD G. ZWEIFEL

IN a recent publication (Zweifel, 1959), I discussed the distribution and variation of lizards related to *Cnemidophorus sacki* and came to the conclusion that previous authors had confused three species in western Mexico under the name *sacki*. For these species I used the names *sacki, communis* and *scalaris*. Since the publication of my paper, information has come to light showing that the name *sacki* properly applies to another species, hence I substitute here the next available name, *costatus* Cope (1877), for *sacki* as it was used in my 1959 paper. Justification for this substitution will be presented in a forthcoming paper (Duellman and Zweifel, Ms.).

On the evidence of specimens available to me, *Cnemidophorus costatus* and *C. communis* were thought to be allopatric, but were treated as species because the differences between them were greater than between some sympatric species of *Cnemidophorus*. Duellman (1960) confirms the specific distinctness of *communis* and *costatus*, which occur together in the Tepalcatepec Valley of Michoacán south of the region I studied. However, the status of *costatus* and *scalaris* as species is questioned by Grant and Smith (1960) who report that these forms intergrade in the vicinity of Guadalajara, Jalisco. On the basis of a smaller sample of specimens than was available to Grant and Smith, I reported (1959:84) that the two forms overlapped without intergradation.

The possibility of intergradation in this region is of more than local interest, as the forms in question represent two distinct subgroups within the *sexlineatus* species group. One of these subgroups, *costatus*, includes a variety of forms found at relatively low elevations in western and southern Mexico. The other, *scalaris*, includes several named and unnamed forms of the Mexican Plateau and peripheral regions. In view of the significance of intergradation between these forms for the taxonomy of a large proportion of the Mexican whiptails, I thought it desirable to review the evidence. Dr. Hobart M. Smith very kindly lent me the specimens in the University of Illinois Museum of Natural History (abbreviated UIMNH) reported in Grant and Smith (1960). These specimens, together with those studied previously and including some newly acquired by the American Museum (AMNH) have been utilized in my restudy of the situation.

Grant and Smith discuss intergradation in terms of *Cnemidophorus sacki huico* and *C. sacki scalaris*, whereas the forms in contact are called *C. sacki occidentalis* and *C. scalaris* ssp. in my 1959 paper. Misinterpretation of color pattern by Grant and Smith, as is explained below, led them to use the name *huico*. All data for *costatus* given here refer to the subspecies *occidentalis* unless specified otherwise.

DORSAL SCUTELLATION

A number of recent studies show that species of *Cnemidophorus* may often be distinguished in terms of the relative size of the dorsal scales. In many, if not most, instances this character offers the surest means of specific identification. My paper characterizes dorsal scutellation by the number of granules around midbody, here abbreviated GAB. Grant and Smith use a similar method, but count only the scales on one side of the body. The data published by Grant and Smith (doubled) agree closely with my own data for the same specimens. Thus discrepancies in our interpretation cannot be at-

tributed to different techniques in making counts.

Grant and Smith report specimens from two localities: Rancho Primavera, ten miles west of Guadalajara, and Barranca de Oblatos on the northeastern edge of the city. Two specimens, UIMNH 46680–81, said to be from Barranca de Oblatos, are reported to resemble typical *scalaris*. According to the field tag, these are from Mascota, almost 100 miles west of Guadalajara. This is well within the range of *C. c. occidentalis* and the high scale counts of these specimens (GAB 95, 102) are consistent with this identification.

The specimens from Barranca de Oblatos are divided into two groups by Grant and Smith, who refer to 22 specimens as *sacki* (= *costatus*) and to nine as being intermediate between *sacki* and *scalaris*. The larger group of specimens has a GAB average of 90.8, range 74–104 (21 specimens counted; one is damaged); counts for the smaller group provide an average of 89.3, range 83–101. The difference between the means is only 1.5 scales and gives little support for an assumption that the samples differ. The average GAB counts given in my paper (1959:107) for *scalaris* in Jalisco and *costatus* from 20 to 30 miles south of Guadalajara are, respectively, 85.6 and 103.3. It is apparent that the samples from Barranca de Oblatos are intermediate in this respect. This could signify a population of intergrades, as Grant and Smith surmise, or could result from the pooling of two distinct populations, with the result that the mean falls somewhere between the true means for each of two distinct entities. If the population is truly intermediate, it would be reasonable to expect a symmetrical curve with the mode approximating the mean. If, however, the data for two different populations have been pooled, a bimodal curve would be expected. I have plotted the data for the specimens Grant and Smith report from Oblatos in a histogram (fig. 1B), to which I have added data from several other specimens from the immediate vicinity of Guadalajara. The resultant histogram for 45 specimens has a distinctly bimodal aspect.

Data for 12 specimens from Rancho Primavera are plotted in fig. 1C. There are too few specimens to establish modality, but the counts are heavily weighted on the high end of the range, in contrast to the picture in fig. 1B.

The data in figures 1B and 1C must be interpreted in light of the scutellation of presumably typical populations of *C. scalaris* and *C. c. occidentalis*. Ideally, these comparative samples should be large and should come from regions not too far removed from the presumed area of intergradation, so that geographic variation will not confuse the picture. These conditions cannot be met fully, but data at hand will probably suffice. As typical of *scalaris*, I have selected 12 speci-

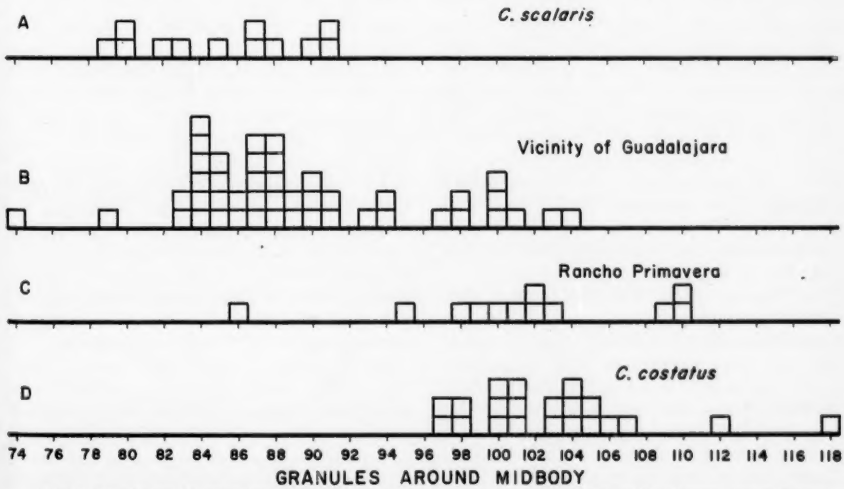

Fig. 1. Variation in number of dorsal granules in four samples of *Cnemidophorus* from Jalisco. Each square represents one specimen.

mens from 30 to 50 miles SSE and SE of Guadalajara along the northern edge of Lake Chapala, north and east of the known range of *costatus*. Scale counts for these are plotted as fig. 1A. The sample of *costatus* consists of 21 specimens from the vicinity of Jocotepec at the western end of Lake Chapala and 18 miles north of Jocotepec. Scale counts for *costatus* are plotted as fig. 1D. The vast majority of specimens from the vicinity of Guadalajara fall within the ranges of variation of either *scalaris* or *costatus*, there being only three intermediates. Similarly, most specimens from Rancho Primavera are in the range of variation of *costatus*, with one typical of *scalaris* and one intermediate. It is important to note that the separation between *costatus* and *scalaris* coincides with the trough in the bimodal curve (fig. 1B), and is not an arbitrary subdivision. Thus 93 percent of these supposedly intermediate lizards can be assigned to one or the other species on the basis of the number of scales around midbody. It cannot be determined whether the remaining four lizards represent the tail of one or both curves, or are hybrids, but in my interpretation the data on scutellation offer no support for the assumption that *scalaris* and *costatus* interbreed freely in the region of Guadalajara.

Color Pattern

The color pattern of large adult lizards frequently provides the best basis for subspecific categories, but many species have similar juvenile and young adult patterns. Even large adults of unrelated and geographically remote forms may develop virtually identical patterns, hence much of the chaotic condition of the taxonomy of the genus *Cnemidophorus* is traceable to improper use of color pattern in working out relationships. In their analysis of the relationships of the *Cnemidophorus* at Guadalajara, Grant and Smith evidently were misled by erroneous interpretation of color pattern.

In diagnosing *Cnemidophorus scalaris*, I (1959:73) was concerned mainly with scale counts and did not discuss geographic variation in color pattern, as this species was largely peripheral to the geographic limits of my study. I included a plate (pl. 48) showing two stages of pattern metamorphosis in a *scalaris* from ten miles north of Chapala, Jalisco, but unfortunately did not specify that the combination of stripes and spots in the later of the two stages was not the terminal pattern of adult males in this region. In specimens approaching maximum size, the stripes on the body fade (but may persist on the neck) leaving a wholly spotted pattern. The presence in their sample of individuals with this pattern evidently led Grant and Smith to assume that *scalaris* intergrades with *C. costatus huico*, which possesses a similar pattern (Zweifel, 1959: pl. 43). A study of the geographic relationships of the forms (ibid.; fig. 1) shows that the ranges of *huico* and *scalaris* are separated by a distance of over 100 miles, and this intervening area is occupied by *C. c. occidentalis*. Grant and Smith comment that the "absence of specimens resembling Zweifel's *C. sacki occidentalis* in both of the present samples is somewhat surprising" (1960:42). Actually, there are several *occidentalis* in the samples, but none is large enough to have developed its terminal pattern (Zweifel, 1959: pl. 47), so was not recognized by Grant and Smith.

Confusion with regard to the terminal pattern of *scalaris* coupled with misunderstanding of subadult pattern led Grant and Smith to conclusions that are essentially the reverse of mine. For example, they cite as "more or less typical of Zweifel's *Cnemidophorus sacki huico*" a specimen from Rancho Primavera (UIMNH 47792) that has a snout-vent length of 89 mm., 86 GAB, and a spotted pattern. Both the scale count and pattern are quite typical of *C. scalaris*. Eleven other specimens from Rancho Primavera "are thought to be more or less typical of *scalaris* in this region since the pattern agrees excellently with Zweifel's figure . . . of a specimen from 10 mi. N Chapala, Jalisco . . ." These specimens have a GAB average of 102.6 (range 95–110). So on this criterion they are typical of *costatus*, with perhaps slight reservation about the single specimen with 95 granules.

Though it is true that the pattern of some specimens is similar to that illustrated for *scalaris*, this is of little significance for the combination of stripes and spots is common to a whole host of species and subspecies, including subadults and young adults of both *costatus* and *scalaris*. Of more pertinence is that even relatively large specimens in this series have strong stripes and obscure spotting. Three measuring 94, 95 and 100 mm. have distinct stripes and moderately spotted fields, whereas *scalaris* of this size typically shows little or no trace of striping. An excellent comparison is provided with UIMNH 47792, mentioned above, and UIMNH 47803. The latter specimen measures 100 mm. S-V,

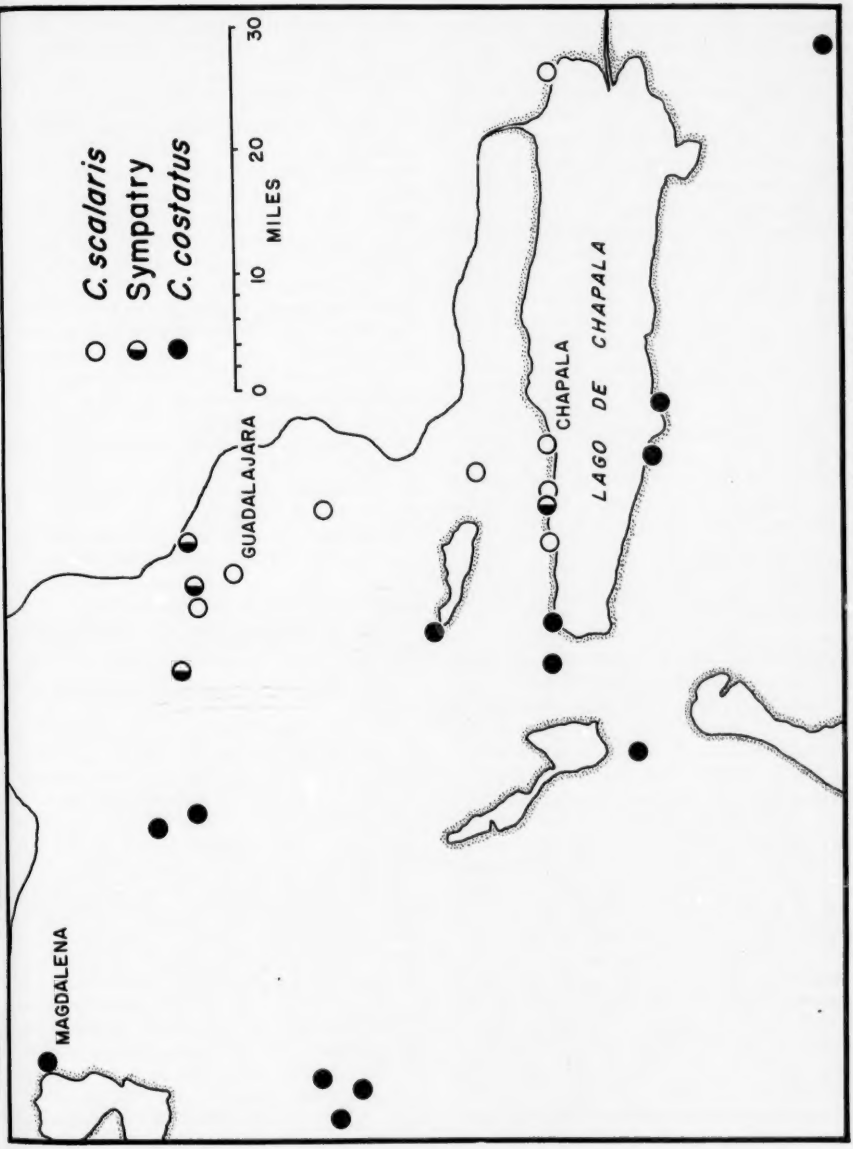

Fig. 2. Distribution of *Cnemidophorus scalaris* and *C. costatus* in the vicinity of Guadalajara and Lake Chapala, Jalisco.

has strong paravertebral and dorsolateral stripes (the laterals are disrupted by vertical bars), and has relatively indistinct spotting in the fields. The typical *scalaris* (47792) at a snout-vent length of 89 mm. retains only a faint trace of the paravertebral stripes on the body and is spotted with no vertical barring on the sides. Another specimen measuring 100 mm. (UIMNH 47796) has undergone more pattern metamorphosis than UIMNH 47803, but significantly not in the direction of the *scalaris* pattern. This specimen has faint paravertebral stripes, but the dorsolateral stripes are broken and the upper lateral field is invaded anteriorly by vertical bars that are well-developed in the lower lateral field. Spotting is well-developed on the posterior part of the body. The spotting posteriorly and barring anteriorly are typical of *C. costatus occidentalis*. The evidence of color pattern, then, does not support the inference of intergradation at Rancho Primavera.

Most of the specimens from Barranca de Oblatos are too small for the characters of pattern to be of significance, but some deserve individual mention. The four largest specimens measure 86 to 88 mm., S-V. Two of these, UIMNH 46678–79, are wholly spotted without stripes on the body or lateral barring. This pattern combined with relatively low scale counts (GAB 85 and 91) confirms their identity as *C. scalaris*. Another in the same size range (UIMNH 46665) is a *costatus* with 98 granules around midbody and, significantly, all stripes strong and distinct and spotting obscure. A specimen of particular interest is UIMNH 46656 which has 94 midbody granules, persistent stripes, and fairly well-developed spotting in all fields except the vertebral. A *scalaris* of this size (S-V 86 mm.) might be expected to show less distinct striping, but the spotting and lack of vertical bars is more typical of *scalaris* than of *costatus*. Whether this specimen is truly a hybrid or merely a variant of one or the other form cannot be said. The other two specimens with intermediate scale counts are too small for the pattern to be of significance.

Despite the relatively large number of specimens (57) available from Guadalajara and vicinity, including Rancho Primavera, the sample is inadequate for final resolution of the intergradation problem from the standpoint of color pattern. There are too few large adult males, and it is in these large individuals that intergradation in color pattern will be manifest if it occurs. The presence of typical *scalaris* pattern both at Rancho Primavera and Guadalajara, however, is noteworthy. A strong tendency toward the ultimate pattern of *C. costatus occidentalis* is seen in other specimens, but none is large enough to have completed metamorphosis.

Other Characters

In addition to the principal characters of dorsal scutellation and pattern there are features mentioned by Grant and Smith that one might infer were significant. These include the presence of a single *versus* a double vertebral line and small as against large postantebrachial scales. For example, the adult *C. scalaris* from Rancho Primavera is said to agree "excellently with *huico* except in the low dorsal scale count, and in having two vertebral light lines" (1960:42), whereas I stated (1959:86) that in *huico* "The vertebral field is most often occupied by a pair of irregular, indistinct, light lines . . ." Similarly, one might infer from Grant and Smith's presentation that *costatus* and *scalaris* differ in relative size of postantebrachial scales, but I stated (1959:71) that in *scalaris*, "The postantebrachial scales are abruptly enlarged, as in [*costatus*]." There is considerable intraspecific variation in this character, and some sexual dimorphism, but Smith and Grant present no evidence that the species differ measurably.

Local Distribution and Abundance

The collections from the immediate vicinity of Guadalajara are composed predominantly of *scalaris*, whereas the sample from Rancho Primavera ten miles to the west is heavily weighted to *costatus* (fig. 1). This may reflect the actual relative abundance of the forms in the two areas, and is consistent with their general distribution. However, both the specific composition of samples of *Cnemidophorus* and the relative abundance of different size classes of *Cnemidophorus* are often strongly influenced by season and weather, as Grant and Smith are aware (1960:42). The absence of large individuals of *costatus* and the relative scarcity of large *scalaris* in Grant and Smith's series from Barranca de Oblatos probably result from the early date of collection, April. In contrast, the lizards from Rancho Primavera were collected in July and all are over 80 mm. S-V length, with seven of the 12 exceeding in length all 31 specimens from Barranca de Oblatos.

Cnemidophorus scalaris and *C. costatus* evidently occur sympatrically along the north

shore of Lake Chapala west of the town of Chapala. There are too few specimens for a meaningful analysis, but the few available suggest a situation similar to that around Guadalajara. Specimens from the east end of the Lake around Jamay are all *scalaris*, and a single large adult male *scalaris* comes from one-half mile west of Chapala. There are four specimens from the vicinity of Ajijic, about four to six miles west of Chapala. On the basis of scale counts, three are referable to *scalaris* (GAB 86, 87, 92) and one to *costatus* (GAB 98). Unfortunately none is large enough for the pattern to be of significance. *Cnemidophorus scalaris* extends westward at least to one mile east of San Juan Cosolá, where C. M. Bogert collected a clutch of eggs from which *scalaris* hatched. The extent of overlap indicated is three or four miles here and at least 12 miles near Guadalajara. Presumably additional collecting will demonstrate a slightly wider zone of overlap and reveal other areas of contact. The southeastern edge of Lake Chapala in particular should be investigated, as *scalaris* occurs on the northeastern edge and *costatus* is present near Jiquilpan, Michoacán, to the south.

Specimens Examined

In addition to the specimens listed in my previous paper (1959:84–5), I have examined the following material, all from the State of Jalisco: *Cnemidophorus costatus occidentalis*: Rancho Primavera, 10 mi. W Guadalajara (UIMNH 47793–47803); Mascota (UIMNH 46680–81); Ajijic (AMNH 82053); Barranca de Oblatos (UIMNH 46653, 46657, 46660, 46665–66, 46671, 46673, 46676); 3.5 mi. S Zacoalco (AMNH 84235–39). *Cnemidophorus scalaris* ssp.: Rancho Primavera, 10 mi. W Guadalajara (UIMNH 47792); ½ mi. W Chapala (AMNH 82049); 1 mi. E Ajijic (AMNH 82050); 2 mi. E Ajijic (AMNH 82051); Ajijic (AMNH 82053); Barranca de Oblatos (UIMNH 46649–52, 46654–56, 46658–59, 46661–64, 46667–70, 46672, 46674–75, 46677–79); 1 mi. E San Juan Cosolá (AMNH 84234).

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The Embryology of *Eleutherodactylus augusti latrans*

Bryan B. Valett and David L. Jameson

THE members of the genus *Eleutherodactylus* have an unusual life history in that they do not pass through an aquatic tadpole stage. The eggs are laid on land and give rise to tiny frogs that, when hatched, show the typical body form of the adult. Surprisingly little is known about the embryology of this genus, but it is clear that various members of the genus differ in the extent to which the anuran larval structures, such as external gills and intestinal coiling, are developed during embryonic stages. In all cases studied by other investigators the larval organs which develop are atypical. The present paper is concerned with a partial study of the embryology of *Eleutherodactylus augusti latrans*.

The first report of direct development in this genus was published by Bello y Espinosa (1871), who briefly recorded finding a cluster of eggs in his garden in Puerto Rico. Subsequently only a few papers have described portions of the development of several species: *portoricensis* (Bavay, 1873a, b; Pêters, 1876; Selenka, 1882; Glitian, 1944), *nubicola* (Sampson, 1904; Lynn, 1942), *inoptatus* and *abbotti* (Noble, 1926), *guentheri* and *nasutus* (Lynn and Lutz, 1946a, b), and *ricordi planirostris* (Goin, 1946).

Materials and Methods

The embryological material used in this study was collected in the Edwards Plateau in Bandera County, Texas. Preliminary observations on the cluster of eggs were reported by

Jameson (1950). The eggs were all in a late stage of development and a complete embryological study was not possible. Several eggs were sectioned and the material compared with previous contributions to the embryology of *Eleutherodactylus*.

A small part of the slides were stained with hematoxylin and eosin routine stain and the remainder in Mallory's triple stain. Frontal and sagittal sectioning was not successful because of the large amount of yolk; transverse serial sectioning provided best results.

Several methods have been used by previous workers to stage *Eleutherodactylus* embryos. Lynn (1942) stages the embryos of *E. nubicola* according to days before hatching, therefore −14 days indicates 14 days before hatching. The eggs of *E. augusti* available for this study correspond to the stage −12 days to −14 days of *E. nubicola* (Lynn 1942) and to stage VII to IX of *Eleutherodactylus martinicensis* (= *E. nubicola*) according to Sampson (1904). Sampson stages the embryos from the first day observed as stage I and hatching as stage XIV. Goin (1947) and Lynn and Lutz (1946a) stage the embryos of *E. planirostris* and *E. guentheri* from the first day observed as the 1st day stage. The *E. a. latrans* embryos correspond to the 8 day stage of *E. ricordii planirostris* according to Goin (1947), and the 7 day stage of *E. guentheri* according to Lynn and Lutz (1946a). Lynn and Lutz (1946a). Lynn and Lutz (1946b) stage embryos of *E. nasutus* from the first day observed as stage I. The *E. augusti* embryos correspond to the stage II of *E. nasutus* according to Lynn and Lutz (1946b).

Stages based on time are subject to environmental modifications which make comparisons of various material very difficult. Certainly the well described stages of *Rana* are more useful than the assemblage of stages available for *Eleutherodactylus*. The material we have available represents only one stage and thus we have refrained from establishing any new system in hopes that adequate stages based on morphological criteria will be forthcoming from those more favorably placed geographically to work on this group. The comparative study which follows must of necessity refer to previously established stages.

Gross Description

The eggs are large, 8 to 8.5 mm, and the embryo covers half of the yolk (see *Copeia*, 1950, p. 44; plate I). The head of the embryo is held above the yolk and the forelimbs extend almost to the tip of the nose. The hindlimbs extend down and away from the body. A thin fold, called the dermal fold by Sampson (1904) and Lynn (1942), covers part of the forelimbs. The head and thorax region is large and wide while the abdominal area as narrow and long to the region of the hindlimbs. Posterior to the hindlimbs the tail begins as a thick area but soon expands into a sheath. The tail has rotated to the right and the expanded sheath of the tail encircles the entire yolk and embryo.

Alimentary System

In *Eleutherodactylus augusti* the condition of the gut is similar to that of the other *Eleutherodactylus*. The long gut is full of yolk granules and the lumen is present only near the cloaca and the esophagus. The gut is a straight tube until it reaches the area of the stomach where it becomes flattened and has several coils. The extensive intestinal coiling found in the typical amphibian is not present. The esophagus is flattened dorsoventrally anterior to the stomach and lacks a lumen. The laryngotracheal groove is in the posterior pharyngeal floor. The stomodeal invagination has broken through into the pharynx forming a mouth. The cloaca is well developed with large openings to the Wolffian ducts.

The yolk is encircled by splanchnopleure; both the endoderm and mesoderm are very thin. The hollow gall bladder is embedded in the periphery of the slightly lobed liver. The bile duct and pancreatic duct drain separately into the gut. The pancreas is a single structure to the left of the intestine.

Sampson (1904) reports that four visceral pouches, I to IV, were found in *Eleutherodactylus nubicola* at this stage but soon disappeared, apparently without opening to the outside to form true gill slits. Lynn (1942) reports that *E. nubicola* has only three pouches with the fourth being rudimentary. Only three very small pouches have been found in *E. augusti*. The small oval thyroid is in the floor of the pharynx and the thymus and the parathyroids have not differentiated.

Nervous System

All parts of the primative brain are well developed. The roof of the rhombencephalon is thin and wide. There is no apparent flexure of the brain. The prosencephalon has differentiated into telencephalon and diencephalon. The large infundibulum is bordered anteriorly by the optic chiasma. The cerebral hemispheres are established. In other

Eleutherodactylus of this stage the brain has reached its final proportional size.

The olfactory nerve joins the telencephalon from the olfactory placodes. Internal nares could not be found. The oculomotor nerves arise ventrally from the midbrain. The other eye muscle nerves are present in rudimentary form. The trigeminal ganglion has established contact with the medulla, and the Gasserian ganglion has differentiated. The facialis and the acoustic ganglia are seen in the region of the ear. The vagus is closely associated with the glossopharyngeal, which is not entirely differentiated at this stage.

The optic cups have well developed retina and lens. The optic nerves are completely formed. The sacculus of the ear is separated from the utriculus. The anterior vertical and horizontal semicircular canals are complete. The posterior semicircular canal, the last part of the labyrinth to form, is not yet present. The large endolymphatic recesses are dorso-lateral to the ear and lateral to the brain. There is no evidence of Jacobson's organ or lateral line organs. Lynn (1942) reports that, though he was unable to find the lateral line organs in *E. nubicola*, Jacobson's organ appears immediately before hatching. Neither Jacobson's organ nor lateral line organs are mentioned in other accounts of the development of *Eleutherodactylus*.

Respiratory System

The highly vascularized tail probably serves as the major organ of respiration in the absence of functional gills. Thick walled lungs are connected to the esophagsu by the laryngotracheal groove. The larynx and glottis are not found at this stage in *Eleutherodactylus nubicola* or *E. augusti*.

Urogenital System

Large pronephroi are present in the anterior region. Several nephrostomes are developed. Lynn (1942) reports that in *Eleutherodactylus nubicola* the head kidney reaches a very large size and persists until hatching. The very convoluted mesonephric tubules can be traced to the Wolffian duct. Mesonephric glomeruli are internal and well developed. The mesonephric tubule area is about ¾ the volume of the pronephric area and extends to the cloaca. The thickened bladder primordium is found in the wall of the cloaca.

Gonadal ridges are present as projections into the coelom from the dorsal mesentery. Mullerian ducts have not been reported in *Eleutherodactylus*.

Vascular System

The heart of *Eleutherodactylus augusti* at stage −14 has a thick ventricular wall and well formed trabeculae. The walls of the atrium are thin. The flexure of the heart is complete. The semilunar valve is not complete; the auriculoventricular valves are present. The truncus is divided by the longitudinal septum. The sinus venosus is an expanded area receiving the cardinals and the posterior vena cava. The sino-atrial opening is bordered by the incomplete sino-atrial valve. The interatrial septum is not yet well developed. This septum, which in other *Eleutherodactylus* is complete at hatching, will separate the small left atrium from the large right one. Sampson (1904) suggested that the late appearance of the interatrial septum may be correlated with the slow growth of the lungs and pulmonary vessels, which are relatively poorly developed even at hatching.

The carotid supply to the head of *Eleutherodactylus augusti* is well established anteriorly to the incomplete circle of Willis. The subclavian arteries can be traced as single vessels to the extremities of the forelimbs. Very small branches supply the area of the forming bone. The vertebrals were not found. The basilar artery is completed later in development. Small arteries from the paired dorsal aortae pass into the glomeruli of the pronephros. The paired dorsal aortae fuse near the level of the pronephros, and just posterior to this fusion the coeliac artery arises. The coeliac artery passes along the right side of the gut, gives rise to small branches to the viscera and then is distributed into the yolk mass. The dorsal aorta continues posteriorly and gives off small branches to the mesonephros. The iliac arteries arise in the region of the hindlimb and continue as single vessels into the distal portion of each limb. Small branches supply the forming bones of the limbs. The dorsal aorta continues into the tail as paired caudal arteries that give off branches to the expanded tail which at this time surrounds the entire embryo.

The pre-cardinal veins extend ventro-lateral to the eye region. The external jugulars from the lower jaw join the common cardinals. The posterior cardinals arise from the tail and join the posterior vena cava in the region of the hindlimbs. The caudal vein receives branches from the tail. The posterior

cardinals and the posterior vena cava, are the main drainage of the trunk area, and by way of the caudal vein, of the tail. The hepatic portal vein enters the posterior portion of the liver. This system drains the intestine. The posterior vena cava and the posterior cardinals give off branches to the mesonephrios. The major changes in the veins occur in *E. nubicola* between −12 days and −10 days (Lynn, 1942). The cardinals lose their connection with the posterior vena cava and dwindle away. The posterior portion of the cardinals forms the renal portal system.

Sampson (1904) and Lynn (1942) found a complete loss of the mandibular and hyoid aortic arches in *Eleutherodactylus nubicola*. Only two of the three arches that form are easily seen in the available *E. augusti* material. These are the carotid and systemic arches. The third, the pulmocutaneous, is very small. The dorsal aortic root between the carotid and the systemic arches has disappeared, and the adult condition of the arches has thus been reached at this stage. The pulmonary vessels are not found and would not be expected until hatching.

Skeletal System

All of the structures are cartilaginous. Each vertebra is represented by a single pair of cartilages which are lateral to the neural tube and beside the notochord. The neural arches have fused to the arches of the centra in the anterior region. No cartilaginous formations are found on the dorsal or ventral side of the notochord.

There is no evidence of pelvic or pectoral girdles. Lynn (1942) did not find the girdles until later in development. The humerus, tibia, fibula and the femur are well chondrified; the radius and ulna rudimentary.

The otic capsules are shell-like structures which enclose most of the labyrinths. Broad connections occur between the otic capsules and basal plate. Internal carotid foramina occur at the posterior end of the trabeculae which are forward projections of the basal plate. A small process from the trabeculae, the pila antotica, extends upward and forward forming the posterior area of the otic capsule. The quadrate cartilage is present but does not connect with the basal plate. Meckel's cartilage is below the quadrate cartilage. The hyobranchial skeleton consists of four pairs of cartilage attached to a broad central plate posterior to the jaw cartilages.

Tail

Lynn and Lutz (1946 b) state that the tail of *Eleutherodactylus nasutus* forms a blade and becomes vascularized but immediately after hatching is absorbed. Lynn (1942) noted in *E. nubicola* that the tail starts its degeneration as soon as the lungs come into function. Lynn and Lutz (1946 a) reported that in *E. guentheri* there is vascularization of the yolk before the tail becomes expanded or vascularized to any extent. There is general agreement that the tail is the main respiratory structure of the embryo.

The tail of *E. augusti* is more expanded than in other members of the genus, and (fig. 1) covers the entire yolk ventrally, passes dorsally over the head and covers the dorsal surface of the embryo posteriorly past the end of the spinal cord. In the caudal region the proximal, lateral and peripheral portions of the tail may be seen (Fig. 2).

Internally, the notochord becomes larger and flattened dorsoventrally near where the spinal cord disappears. Posterior to this the notochord and the tail rotate to the right. Further posteriorly the notochord disappears while the tail continues as the expanded sheath. The right side of the tail is external and the left side is internal. From the exterior to the interior are three cell layers: the right tail ectoderm, vascularized mesoderm and left tail ectoderm.

The enveloping nature of the tail appears to serve a function structurally like the amnion of higher forms and perhaps offers an explanation of how the amnion might have originated. However, the vascular nature of the somatopleure is not characteristic of amniote extra-embryonic membranes.

Discussion

Cleavage in *Eleutherodactylus* was described by Goin (1947) and Glitian (1944) and briefly by Sampson (1904). Equatorial cleavages are lacking; the early cleavages began at or near the animal pole and move vegetally. In *E. portoricensis* the first cleavage furrow begins at the animal pole and is complete before the second begins. The second cleavage furrow is at right angles to the first. The third and fourth cleavage furrows begin on either side of the second before the second cleavage plane is complete. The fifth and sixth cleavage furrows are at right angles to the second, third and fourth cleavage plane. Cleavage from this point on is very complex

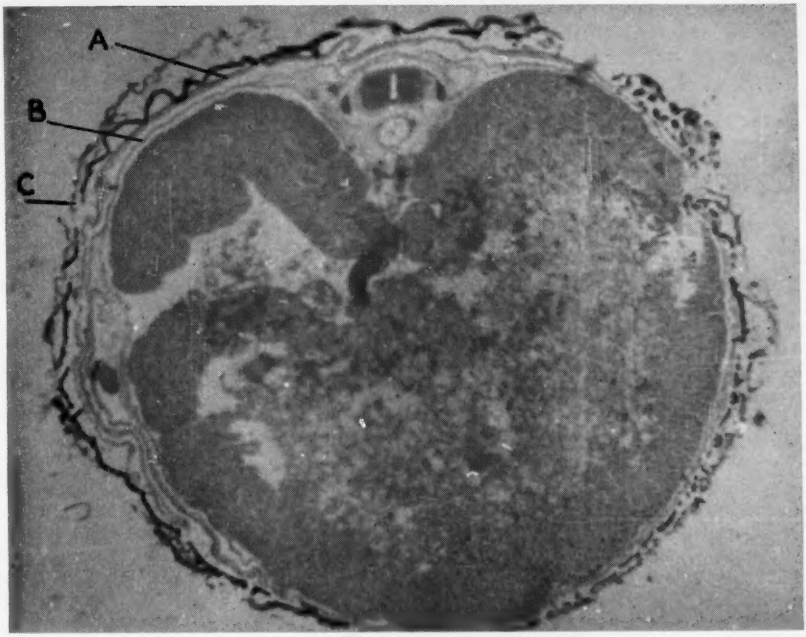

Fig. 1. Cross section of embryo *Eleutherodactylus latrans* at mid body; A. ectoderm of left side of expanded tail, B. ectoderm of embryo body, C. ectoderm of right side of expanded tail.

with the animal cells dividing periclinally. The segmentation cavity forms early in cleavage in the upper one-third of the egg. Gastrulation is accompanied by a yolk-plug. The neural plate thickens and development continues. Cleavage in *E. ricordi* is holoblastic and unequal and differs from that of *portoricensis* in that the third cleavage furrows are on each side of and parallel to the first while in *portoricensis* the third and fourth furrows are parallel to the second. Sampson (1904) notes that *nubicola* also lacks equatorial furrows.

Lynn and Lutz (1946 a) staged embryos of *Eleutherodactylus guentheri* from the first stage found. These eggs showed cleavage furrows. On the fifth day the neural plate was well developed. On the twelfth day limbs and a tail bud were present. On the fourteenth day blood circulation was observed and the eyes were pigmented. At the eighteenth day the embryo was mobile with a large expanded tail. On the twenty-third day the small egg tooth was formed and the heart was seen. On the thirty-third day the embryo

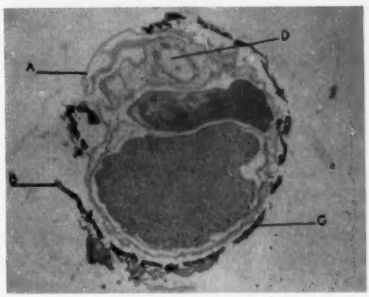

Fig. 2. Cross section of embryo *Eleutherodactylus latrans* near base of tail; A. proximal portion of tail, B. peripheral portion of tail, C. lateral portion of tail, D. dorso-ventrally flattened notochord.

appeared as a small frog. Embryological study revealed that gills, gill slits, operculum, tadpole-like mouth parts, and typical intestinal coiling were not present. Simplified aortic arch development, a modified tail and an egg tooth were evident. Embryonic development in *Eleutherodactylus nasutus* (Lynn and Lutz,

1946 b) is similar to that of *Eleutherodactylus guentheri*.

Sampson (1904) and Lynn (1942) described the embryology of *Eleutherodactylus nubicola*. The stages described by Sampson progress from I to XV. This corresponds to stages −23½ to one hour after hatching, according to Lynn (1942). At stage −23 the neural tube is just formed and the gut is open to the yolk. The notochord has differentiated. At stage −21 the brain has formed its divisions and the optic cups have appeared. At stage −15 the nerve centers of the brain are present and the cranial nerves are developed. The optic vesicles, with their lenses and optic nerves are present. The ear has been divided into its ultimate parts and the endolymphatic ducts are present. The nasal pits and the olfactory nerve are present. The tail is expanded and highly vascularized. At stage −6 the central nervous system is completely formed and the peripheral nerves have established contact with the brain. The egg tooth is forming. No external or internal gills are found, and the dermal fold is seen covering part of the forelimbs. The embryo is ready for hatching. Upon hatching the lungs come into function, and the pulmonary vessels are easily seen.

The embryonic development of most *Eleutherodactylus* follows the pattern of *E. nubicola* and *E. guentheri* with little variation, though several exceptions are found. Glitian (1944) reported that *Eleutherodactylus portoricensis* has external gills during its embryonic life and Noble (1925) reports that *E. inoptatus* has external gills. A possible explanation of this fact is that the tail in these two species does not grow and expand in proportion with the growth of the rest of the embryo. These external gills appears early in development and also disappear early. The disappearance is correlated with the growth of the tail which has, at the time of disappearance, expanded in proportion with the embryo.

The time from cleavage to hatching in *Eleutherodactylus* varies from species to species. In *E. augusti* it is reported to be approximately 25 to 35 days (Jameson, 1950). Lynn and Lutz (1946b) report the embryonic time to be about 28 days in *E. guentheri* and *E. nasutus*. Glitian (1944) describes the period to be 17.5 and 19.5 days in *E. portoricensis*. Lynn (1937) reports that the hatching time in *E. alticola* is 20 to 21 days.

The process of hatching has been described by several workers. In all the *Eleutherodactylus* investigated there is an egg tooth present, either well developed or rudimentary, directly over the premaxillary symphysis. Ventral suckers have not been reported. Noble (1925) described the hatching in *E. abbotti* and *E. inoptatus* and found that moisture was necessary for the hatching of *E. inoptatus*.

All of the young hatchlings of the *Eleutherodactylus* are reported to be very small; in several cases about the size of a house fly. The hatchlings all appear fully formed with four limbs and typical adult characteristics.

Summary

The embryology of *Eleutherodactylus augusti* coincides closely with that of *E. nubicola* and with other members of the genus. The most striking difference is the fact that the tail covers the entire embryo. Many important changes have occurred in the embryonic evolution of the genus. The particular features of *Eleutherodactylus* are as follows: 1. There is no evidence of ventral sucker, internal gills, horny tadpole mouth parts, lateral line system, true operculum or equatorial cleavages, all of which are typical features of anuran development. 2. External gills, if present, are ephemeral. 3. The tail is modified for use as a respiratory organ. 4. The development of the aortic arches is simplified. 5. An egg tooth is present at the tip of the snout.

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DEPARTMENT OF ZOOLOGY, SAN DIEGO STATE, SAN DIEGO, CALIF.

HERPETOLOGICAL NOTES

WINTER SURVIVAL OF HATCHLING PAINTED TURTLES IN NORTHERN MINNESOTA.—On June 15, 1959 I observed a painted turtle (*Chrysemys picta*) laying eggs at Lake Vermilion in northern St. Louis County, Minnesota. The site, exposed to the sun most of the day, was a fairly level, mowed lawn at the top of a parklike point, some seventy yards from the water and twenty feet above the lake and only six inches from a large boulder that measured four feet across and protruded a foot above the lawn. Cold weather arrived early with temperatures down to zero early in November. Snow cover was even less than normal with probably a foot to sixteen inches of snow covering the nest site most of the winter. The boulder was partly exposed much of the time.

On the following April 15 I dug down and found a live baby turtle halfway out of the topmost egg which was one and a half inches below the surface. The shell looked as if it had been open for some time as the edges were yellowed. This turtle had an egg tooth and its ventral cleft was well open although no yolk was evident.

I re-covered the cavity and expected the turtles to emerge as soon as a few hot sunny days had warmed the ground. However, on May 23 I dug again uncovering two little turtles that scrambled almost imediately out of the hole. Their clefts were open but they had no egg teeth.

Finally on June 15 I dug up three more turtles, all dead but not decomposed, and two empty eggs. The nest cavity was a mass of roots, which may have interfered with the little turtles' emergence.

The above observations were made and recorded at the suggestion of Dr. W. J. Breckenridge, director of the Museum of Natural History at the University of Minnesota.—ED WOOLVERTON, *Cook, Minnesota*

FOOD NOTES AND RECORDS OF THE ATLANTIC RIDLEY TURTLE (*LEPIDOCHELYS KEMPI*) FROM LOUISIANA.—As a further contribution to the intensive study of the distribution of the ridley turtle, *Lepidochelys kempi* (Garman) by students of zoogeography and herpetology, especially Dr. Archie Carr (1942, *Proc. New England Zool. Club 21:1–16*; 1954, *Yearbook Amer. Phil. Soc. p. 138–40*; 1955, *Animal Kingdom 58:146–156*; 1957, *Rev. Biol. Trop. 5:45–61*; Carr and Caldwell, 1956, *Am. Mus. Nov. 1793:1–23*), we are presenting these data on its occurrence in Louisiana coastal waters. Liner (1954, *Proc. La. Acad. Sci. 17:65–84*) reported the capture of 11 ridley turtles in Gulf waters of Terrebonne Parish in 1952. Three of the specimens were catalogued in the Tulane University Collections at the time of his publication but are now missing. Three of the remaining eight animals were later added to the Tulane Collections (TU15218, 15219, 15220); the others are not available for study. These 11 specimens, one from the personal collection of Dr. N. C. Negus and R. K. Chipman, one additional record from the Tulane Collections, and one reported by Carr and Caldwell (1958, *Rev. Biol. Trop. 6:* 245–262) make a total of 14 ridleys captured in Louisiana coastal waters from 1952–1958. The materials studied were skeletal elements—carapace, plastron, and skull.

TU 15218. ♀, weight 38½ lbs., April 25, 1952, 20 mi. W. Oyster Bayou, 12 mi. offshore, captured while trawling for shrimp in Terrebonne Parish waters, coll. E. A. Liner.

TU 15219. ♀, weight 58½ lbs., April 25, 1952, 20 mi. W. Oyster Bayou, 12 mi. offshore, captured while trawling for shrimp in Terrebonne Par.

waters, contained small unfertilized eggs, coll. E. A. Liner.

TU 15220. ♀, no weight, April 25, 1952, near Last Island (Isle Derniere), captured while trawling for shrimp in Terrebonne Par., coll. E. A. Liner.

TU 16831. sex and weight unknown, June, 1954, Lake Borgne, St. Bernard Par., La., coll. unknown.

N. C. Negus specimen. sex and weight unknown, 1958, found dead on Breton Island, Plaquemines Par., La., at the extreme edge of the tidal line, coll. N. C. Negus and R. K. Chipman.

Individual measurements (in mm.) of skeletal elements are in Table 1.

The stomach and intestinal contents of two specimens (TU 15218, TU 15219) are available in the Tulane University collections and provide some idea of the diet and feeding habits of the ridley turtles. The principal elements of both were moderately macerated fragments of exoskeleton of cancroid crabs of the genus *Callinectes*, but small molluscs, muscle tissue, plant parts and mud were also encountered.

In one specimen the collector, E. A. Liner, reports that all the crustacean remains, except "a half crab" which was taken from the stomach, were recovered from the intestine. From these intestinal contents we were able to secure several male abdominal appendages in good condition. The appendages were found to be compatible with those of *Callinectes sapidus* and *C. ornatus* as described and illustrated by Mary Rathbun (1930, *USNM Bull. 152*). In addition, gastropods of the genus *Nassarius* were seen, but were too badly eroded to be identifiable to species. A few twigs, a small fragment of dicot wood, and a leaf resembling the genus *Quercus* were found.

A richer molluscan fauna was recovered in the sample of intestinal remains from TU 15219.

TABLE 1. SKELETAL MEASUREMENTS OF *Lepidochelys kempi* CAUGHT IN LOUISIANA WATERS

Element	TU 15218	TU 15219	TU 15220	TU 16831	NCN
Maximum skull length	161	177	176	97[1]	179
Max. skull width	113	120	126	70	120
Condyle – premax. length	118	129	137	78	130
Max. carapace length	492	497	548	290	—
Max. carapace width	497	506	572	294	—
Plastron length along curve	381	382	421	237	—

[1] Supraoccipital process broken.

Nassarius was represented, as were three genera of clams: *Nuculana*; *Corbula*; and a mactrid clam, probably of the genus *Mulinia*. This gut also contained several mud balls of about two millimeters diameter.

Both specimens from which gastro-intestinal contents were examined were caught at the same locality on the same date. The molluscan fauna suggests that the two ridleys had fed near a mud bottom in an estuarine or bay situation.

The authors wish to acknowledge with thanks the assistance of E. A. Liner for his loan of field notes and Dr. Harold E. Vokes for confirming the diagnoses of the molluscs.—JAMES L. DOBIE, *Department of Zoology, Tulane University, New Orleans, Louisiana*, LARRY H. OGREN, *Department of Biological Sciences, Loyola University, New Orleans, Louisiana*, and J. F. FITZPATRICK, JR., *Department of Zoology, Tulane University, New Orleans, Louisiana.*

RATES OF DESICCATION AND REHYDRATION OF EGGS IN A TERRESTRIAL SALAMANDER, *PLETHODON CINEREUS*.—The egg is commonly considered to be one of the most vulnerable stages of the life cycle, particularly in terrestrial amphibians whose eggs are laid in non-aquatic situations and yet lack a protective shell. In the terrestrial salamander, *Plethodon cinereus*, the eggs usually hang from the roof of a cavity inside or under logs, and are frequently in partial contact with the surrounding materials. Whether such an egg can absorb water may be of importance to its survival. Also of possible significance is the absorption of water from, or loss of it to, the body of the female, which curls around the eggs and remains with them throughout the developmental period. The ability of eggs of a terrestrial amphibian to absorb water has not been previously studied quantitatively. For this reason the following experiments were carried out.

On August 14, 1958, a clutch of nine eggs was taken from relatively dry wood of a pine log in an oak-pine-aspen forest near The University of Michigan Biological Station. The salamanders inside the egg membranes were nearly at the hatching stage. Because the site was so dry for eggs of this species the clutch was taken to the laboratory. It had a total weight of 0.83 gm. Further desiccation to 0.78 gm. was permitted, following which the eggs were wrapped in a damp paper towel for six hours. At the end of this period the total weight was 0.95 gm., representing an increase of 0.17 gm. (17.9 per cent of the final hydrated weight), or approximately 0.03 gm. of water per gram hydrated

weight per hour. The embryos survived this desiccation and rehydration.

A second experiment was carried out in 1959 using an analytical balance. Five clutches of eggs were collected in hemlock logs of the same region on August 3 and transported to the laboratory in plastic bags filled with wet hemlock wood. All were in a late stage of development and appeared in good condition. They were weighed, allowed to desiccate under laboratory conditions (67% relative humidity, 22° C.) for one hour and weighed again, after which each clutch was surrounded by wet paper towels and placed in a petri dish for an additional 9 hours. They were then blotted with dry towels, care being taken to remove the water between individual eggs, and weighed a final time.

Rehydration rates ranged from 0.0034 to 0.0213 gm./gm./hr. However, the values for clutches one and five are misleading apparently because the eggs were not fully hydrated when collected as indicated by more than 100 per cent recovery of the water lost (Table 1). Initial weight was used as a basis for calculation of absorption rates and hence clutches which were not fully hydrated when collected gave excessive values, the error being proportional to the amount of desiccation the eggs had previously undergone (Fig. 1). Thus, only clutches two, three, and four, which had recoveries of 41.0–59.8 per cent, give a true indication of absorption rate. In these three clutches rate of water uptake was 0.0034, 0.0051, and 0.0082 gm./gm./hr.

Table 1. Desiccation and Rehydration of Five Egg Clutches of *Plethodon cinereus*

Clutch No	1	2	3	4	5
No. of eggs in clutch	7	5	3	7	6
Initial weight of clutch in grams	0.6726	0.4310	0.2695	1.1150	0.6058
Loss in grams	0.0480	0.0376	0.0324	0.0843	0.0493
Gain in grams	0.0738	0.0200	0.0194	0.0345	0.1159
Recovery in per cent of water lost	154.0	53.3	59.8	41.0	235.0

The amount of water lost ranged from 7.14 to 12.04 per cent of the initial weight, representing rates of loss of 0.0714 to 0.1204 gm./gm./hr. However, individual eggs in the center of the clutch probably lost less water and those on the periphery more than the figures indicate. All eggs survived the treatment and four of the clutches hatched on August 6. The average vital limit of adults of this species is 25.88 per cent of hydrated weight (Littleford *et al.*, 1947. *Ecol. 28:440–447*).

When the rate of water loss is compared to that for absorption at approximately the same temperature (Fig. 1), it is seen that (1) evaporative rate is much higher, indicating that water is lost more rapidly than it is recovered and that (2) there is a strong correlation of clutch size with rates of absorption and loss. Because of the greater surface area per unit volume of small clutches as compared to large ones, this relationship is expected.

In contrast to absorption rates, there was no significant difference in rate of loss between clutches that were fully hydrated at the beginning of desiccation and those of equal size that had already lost water (Fig. 1). This result indicates that desiccation rate does not change with increased drying and that water freely evaporates from the eggs in the range of moisture

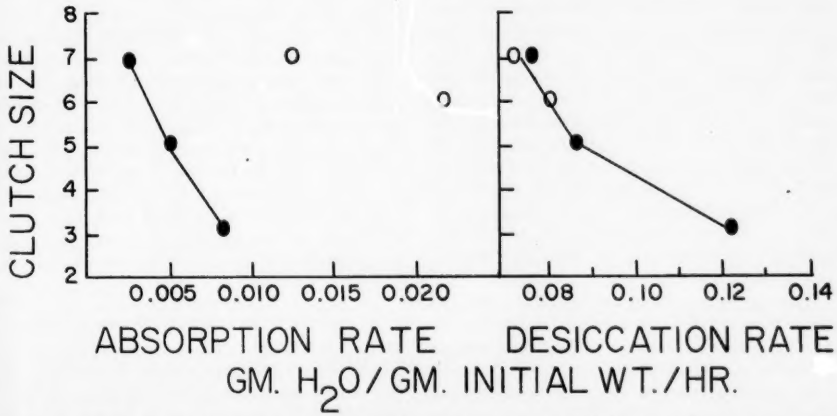

Fig. 1. Relation of clutch size to rates of water absorption and loss in eggs of *Plethodon cinereus*. Open circles—partially dehydrated clutches. Solid circles—fully hydrated clutches.

content of the present study. This lack of any mechanism for preventing evaporation adds significance to the ability of the eggs to absorb water from a damp substrate and correlates with the tendency of *P. cinereus* to oviposit in moist situations.—HAROLD HEATWOLE, *Department of Biology, University of Puerto Rico, Rio Piedras, Puerto Rico*

AN OLDER NAME FOR *THAMNOPHIS CYRTOPSIS* (KENNICOTT).—*Eutaenia dorsalis* was named by Baird and Girard (*Cat. N. Amer. Rept., Pt. 1, Serpents, 1853:31*). The name was originally based upon a single specimen. According to the describers this specimen was collected between Monclova, Mexico, and the Rio Grande, by General S. Churchill. Total length was 25¼ inches, tail 6¼ inches. There were 166 ventrals, 81 subcaudals and 19 scale rows. Probably colors were already somewhat altered by preservative at the time the description was made. The following characters of pattern and coloration were mentioned: Sharply defined, greenish-white dorsal stripe including middorsal scale row and half of each adjacent row; lateral stripe on second and third rows; dorsolateral areas bright olivaceous, with a series of approximately 74 large indistinct spots on each side just above the lateral stripe; ventral surface greenish white with black dots on lateral edges of ventral scutes.

Cope (1900, *Ann. Rept. Smiths. Inst. for 1898: 1076* applied the name *Eutaenia sirtalis dorsalis* Baird and Girard to a subspecies in the Rio Grande Valley of New Mexico. Smith (1942, *Zoologica 27:98)* allocated the name *dorsalis* as a synonym of *Thamnophis sirtalis parietalis* (Say). The characters mentioned in the original description of *dorsalis* are not sufficiently diagnostic to fix with certainty the identity of the type specimen. Since few characters were mentioned, and the range of variation (individual, secondary sexual and geographic) is considerable in the garter snakes, the type might have been any one of several kinds. Its identity must be decided on the basis of greatest probability with the meager information available. We are informed by Dr. Doris M. Cochran that the specimen has long been missing from the U. S. National Museum, and its rediscovery now seems unlikely.

The type was collected by General Churchill (then a colonel) while he was a member of the United States invasion forces that entered Coahuila at the time of the U. S.—Mexican War. According to Jenkins (1851, *History of the War Between the U. S. and Mexico, p. 186*), the invasion route extended westward from San Antonio to the Rio Grande opposite Presidio and south in Mexico through Nava, San Fernando, Santa Rosa, Monclova, Saltillo and Agua Nueva in a course that approximated that of modern Highway 57.

The invasion expedition passed through a desert region in which water was scarce. Habitat for garter snakes would have been found only along the Rio Grande and its tributaries, and various springs and waterholes. Besides the type of *dorsalis*, other herpetological specimens brought back by Churchill and donated to the National Museum included one of *Phrynosoma modestum* and two of *P. cornutum*, all labelled "Rio Grande west of San Antonio".

Thamnophis marcianus and *T. sauritus* both occur in Coahuila but both are readily eliminated from consideration as being conspecific with *dorsalis* on the basis of the characters of color pattern and lepidosis mentioned in the original description of *dorsalis*. Also, there is little likelihood that the type of *dorsalis* was a specimen of *Thamnophis sirtalis*. The color pattern described for *dorsalis* fits *sirtalis* poorly and the scale counts fit only the extremes of that species. Furthermore, the invasion expedition while in Mexico did not travel within 300 miles of the known ranges of either subspecies *(annectens* and *parietalis*) of *T. sirtalis* found in Texas. Interpretation of *dorsalis* as *sirtalis* would necessitate the assumption that it was based on an atypical specimen, and further, that the specimen was mislabelled as to locality.

It seems far more logical to assume that the type of *dorsalis* was a specimen of the garter snake later named *Eutaenia cyrtopsis* (Kennicott, 1860, *Proc. Acad. Nat. Sci. Philadelphia 12:333–334*). Eastern Coahuila is a region of intergradation between *Thamnophis cyrtopsis cyrtopsis* and *T. c. ocellata*. The type of *cyrtopsis* agrees well with such intergrades in both scale counts and color pattern, and we believe it should be so considered unless and until evidence to the contrary comes to light. *Thamnophis cyrtopsis cyrtopsis* thus becomes a synonym of *Thamnophis dorsalis dorsalis*. The other subspecies become *T. dorsalis ocellata, T. dorsalis cyclides, T. dorsalis postremis* and *T. dorsalis sumichrasti*. —HENRY S. FITCH, *Department of Zoology, The University of Kansas, Lawrence*, and WILLIAM W. MILSTEAD, *Department of Zoology, University of Kansas City, Missouri.*

ANOTHER METHOD OF INCUBATING REPTILE EGGS.—Judging from the continuing appearance of articles describing ways of incubating reptile eggs artificially, no system yet proposed has proved universally satisfactory. The method described here undoubtedly is not a panacea for all troubles besetting artificial in-

cubation, but it has some advantages over other means currently in use.

The usual method of incubation involves burying the eggs in a medium such as moistened sand or rotten wood in a rigid container with a tight lid. Details of this general method are given by Shaw (1960, *Brit. Jour. Herp. 2:183*) and Rothman and Rothman (1960, *Bull. Philadelphia Herp. Soc. 8:19–20*). Legler (1956, *Herpetologica 12:290*) modifies this method by using layers of cotton in place of sand or wood, and Carpenter (1960, *Herpetologica 16:179–182*) describes a more elaborate method in which the eggs are placed on sand in a container which is then buried in a large sand box.

The chief difficulties with these methods are that the eggs are not readily observable without disturbance, and the moisture level may be difficult to check or control. Mold often grows to the detriment of the eggs, and attempts by chemical means to deter this growth have met with questionable success.

The method I have used several times over four years differs mainly in that the container is a flexible, transparent plastic bag (1½ mil polyethylene) and the eggs rest on the medium rather than being buried in it. The exact nature of the incubating medium seems to be relatively unimportant; it acts merely as a moisture reservoir. I have used rotten wood in which skink eggs were found, sand, sandy soil and sphagnum moss, and suspect that a sponge would serve adequately. The medium is prepared by soaking it in water and then squeezing out most of the water. It is then placed in the bag and the eggs shallowly imbedded in it. Too wet a medium is to be avoided, though the danger is less acute here than if the eggs were buried in the material. The bag is inflated slightly and then sealed with a rubber band.

Saturation of the atmosphere within the bag is indicated by condensation on its inner surface. Unless the incubation period is very prolonged, it is usually unnecessary to add more water. The general well-being of the eggs can be observed through the plastic, so unless measurements of the eggs need be taken the bag can be left closed until the eggs hatch.

All eggs in eight clutches of skinks (*Eumeces* and *Scincella*) and *Cnemidophorus* collected in the field and incubated in this way hatched successfully. Many of these clutches had undergone most of their development prior to collection, but two clutches of *Cnemidophorus* eggs were in the bags almost 80 days, and a clutch of *Scincella* eggs was in 32 days.

The method has also been applied successfully to eggs laid by captive lizards. Five of six *Cnemidophorus* eggs hatched after 109 days; the egg that failed to hatch did not develop and possibly was infertile. Mr. Charles J. Cole, to whom I am indebted for the use of his data, had approximately 73 percent success with five clutches of *Sceloporus* eggs laid in captivity, though some of the lizards died partly hatched. I exclude from the above figures two clutches of *Sceloporus* in which there was no hatching. One of these had been delivered by Caesarian and the other was inadvertently placed in a bag where the medium was far too wet. Aside from these two clutches of *Sceloporus* eggs, there has been only one conspicuous failure: a clutch of *Coluber* eggs buried in the medium and kept in the dark became moldy and none hatched. All other clutches have been virtually free from mold, a circumstance that I attribute to their being kept in the light and unburied.

An experience in our laboratory suggests one possible source of trouble. When a clutch of *Pituophis* eggs was first observed after hatching, one hatchling was missing, evidently having escaped through a slit in the bag. There was no obvious reason why the bag should have ruptured of its own accord, and I suspect that the snake slit the thin plastic with its egg tooth. It might be advisable to keep a plastic bag containing snake eggs in a snake-tight container.—RICHARD G. ZWEIFEL, *Department of Herpetology, The American Museum of Natural History, New York 24, N. Y.*

Ichthyological Notes

UTILIZATION OF THE NESTS OF GREEN SUNFISH (*LEPOMIS CYANELLUS*) BY THE REDFIN SHINER (*NOTROPIS UMBRATILIS CYANOCEPHALUS*)[1].—A study was initiated in the spring of 1959 on the spawning behavior of the northern redfin shiner, *Notropis umbratilis cyanocephalus* (Copeland). In 1954 this minnow was introduced into one of the University of Wisconsin Arboretum Gardner Ponds, in which a population of green sunfish, *Lepomis cyanellus* (Rafinesque), was already established.

Sexual dimorphism is very noticeable in these

[1] Supported in part by a grant from the Wisconsin Conservation Dept; contributions from the University of Wisconsin Arboretum, No. 48.

minnows during the reproductive period. The males at this time have highly developed breeding tubercles, making the entire head appear powder-blue when viewed from above, and their fins are bright red in color. The females retain their steel-blue coloration throughout the year.

During the breeding season the males appear over the spawning ground in dense swarms. There is no obvious orientation of the individuals to each other in the group and their appearance is reminiscent of that of a swarm of bees. Each male in the swarm is very active and appears to be aggressive towards other male members of the group. The females, on the other hand, remain in deeper water and only occasionally will one or two move through the swarms of males. At this time the female is usually pursued by several males. The males did not show nest-building activity but rather appeared in swarms over nests constructed, and occupied, by male green sunfish. There, only rarely would the male green sunfish respond aggressively toward them. However, if a small green sunfish came near the nest it was immediately chased. On some occasions when there were only a few minnows present on the spawning ground, we observed individual male redfin shiners guarding territories which included an occupied green sunfish nest. The minnow would swim above the nest, often moving completely around its edge. Whenever another male minnow appeared in the vicinity it would be chased vigorously.

A sampling program was initiated in order to determine whether or not minnows were utilizing the nests of green sunfish as spawning sites. The spawning area was sampled by placing watch glasses (150 mm. diameter), outside, as well as inside, of occupied and unoccupied green sunfish nests. The char studied by Fabricius and Gustafson (1954, *Inst. Freshwater Res. Drottningholm Rept. (35):58–104*), was found to spawn even though the substrate was covered by glass; it was hoped that the minnows would also continue to spawn under this condition. Between June 10 and August 1, 1959 the watch glasses were distributed daily and collected the following day. On occasions when no eggs were found, and conditions had not changed, the watch glasses were permitted to remain in place. If eggs were found on any watch glass, all glasses were removed and a new set distributed. The eggs on each watch glass were counted and the young from all samples were raised to the postlarval stage, at which time identification of the two species could easily be made. The larval redfin shiners were much more darkly pigmented than the green sunfish larvae and the shape of the head and jaw of the redfin shiner larvae was markedly different from that of the sunfish. When all of them had reached the postlarval stage the number of both species in the sample was counted. The average mortality for all samples was 54 percent. The mortality of eggs collected at times when only minnows were spawning appeared to be no different from the mortality when both species were spawning.

Table 1. Occurrence of Eggs of *Notropis umbratilus* and *Lepomis cyanellus* on Watch Glasses Placed Inside and Outside of *Lepomis cyanellus* Nests

Location of watch glass	No. watch glasses without any eggs	No. watch glasses with only *Notropis* eggs	No. watch glasses with only *Lepomis* eggs	No. watch glasses with *Notropis* & *Lepomis* eggs	Total watch glasses
In guarded nest	14	5	4	15	38
Outside of nest	52	0	0	5	57

Significantly more plates contained minnow eggs when they were located in guarded green sunfish nests than when they were located outside of the nest or in unoccupied nests (Table 1).

Occasionally green sunfish, while spawning, will move a few centimeters outside of the rim of the nest. Watch glasses located outside of guarded green sunfish nests were found to contain either eggs from both species or no eggs at all. Also, more of the watch glasses located within sunfish nests contained eggs of both species than contained eggs of only one species (Table 1).

Swarms of minnows appeared more often over the nests of spawning green sunfish or over a nest in which spawning had recently occurred, as indicated by the presence of an extremely aggressive male green sunfish, than over the nests of complacent males. The minnows nearly always remained at least 10 cm. above the substrate and were never observed eating any of the eggs in the sunfish nests. If spawning redfin shiners are most often attracted to a green sunfish nest in which spawning is occurring, or has recently taken place, the redfin shiner larvae would be afforded the maximum duration of protection by their foster parents. Research currently under way may determine whether or not this condition exists and, if it does, what the factor is which produces this response by the minnow.

The utilization of the nests of other species by minnows has been described before (Raney, 1940, *Zoologica 25(1):1–14*; Lachner, 1952, *Am.*

Midland Nat. 48(2):433–66), but in these instances the minnows in question were spawning over the nests of other cyprinids. Latta (1958, *Ph.D. Dissertation, Univ. Mich.*) has reported, however, that he observed common shiners (*Notropis cornutus*) spawning in the nests of smallmouth bass (*Micropterus dolomieui dolomieui*). This is, to our knowledge, the only other account of cyprinids utilizing the nests of fishes belonging to a different family. Furthermore, except for the case observed by Latta, none of the fish which have been reported to serve as the host in this type of relationship have the behavior pattern of guarding their eggs after they have been deposited.

Whether or not *Notropis umbratilis* utilizes the nests of green sunfish as a spawning site throughout its range is apparently unknown. However, the fact that the ranges and the habitat preference of the two species closely coincide (Woods, personal communication), indicates that this relationship between them may be fairly widespread.—JOHN R. HUNTER, *Hydrobiology Laboratory, University of Wisconsin, Madison, Wisconsin* and WARREN J. WISBY, *The Marine Laboratory, University of Miami, Miami, Florida.*

AN EASTWARD EXTENSION OF THE WINTER MOVEMENT OF THE MACKEREL, *SCOMBER SCOMBRUS*.—The capture of one mature and three immature Atlantic mackerel, *Scomber scombrus* Linnaeus, in an otter trawl on March 10, 1960, approximately 180 miles east of Nantucket Island at 41° 24′ N. and 66° 01′ W. in 101 fathoms of water, extends the known eastward, or offshore, winter movement by nearly 100 miles. A bottom temperature of 44.1°F. was recorded by means of a bathythermograph at the end of the half-hour tow. At the same time the surface temperature was 40.9°F.

The mature mackerel measured 41.0 cm. from snout to the fork of the tail; the three immature fish were, unfortunately, lost before they could be closely examined.

The winter range of the Atlantic mackerel as assumed by Sette (1950, *U. S. Fish and Wildl. Serv. Fish. Bull. 51(49):259*), was offshore to about the edge of the Continental Shelf in the deeper water where winter water temperatures are suitable. He had, however, no direct evidence that mackeral were to be found there. His table of winter capture records indicates that no fish had been taken east of 68° 00′ W. longitude in the vicinity of Georges Bank.

Bigelow and Schroeder (1953, *U. S. Fish and Wildl. Fish. Bull. 53(74):320*) state that temperature evidence supports the assumption made by Sette and that mackerel probably winter 30 to 100 miles offshore in water 50 to 100 fathoms in depth and a water temperature of approximately 44° to 46° F.

Fishing effort is at a minimum on the eastern edge of Georges Bank during the winter months, particularly in water deeper than 50–75 fathoms. It is probably for that reason that no records of the offshore limits of the mackerel are available for the colder months.—JOHN B. SKERRY, *U. S. Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Massachusetts.*

PARAMYRUS KELLERSI FOWLER, A SYNONYM OF THE EEL *CONGER CINEREUS CINEREUS* RÜPPELL.—In 1932 Fowler described a new species of eel *Paramyrus kellersi* in the family Echelidae (*Proc. U. S. Natl. Mus. 81(2931):1–2, fig. 1*). The eel was obtained by Lieutenant H. C. Kellers, of the U. S. Naval Eclipse Expedition of 1930, at Niuafo'ou Island, Tonga Group in Oceania, on September 17.

On reexamination of the holotype of *Paramyrus kellersi*, USNM 91870, it was found to be a young eel which was slightly mutilated; however, certain features are still recognizable so that it could definitely be identified as *Conger cinereus cinereus* Rüppell. Fowler stated that the posterior nostril is on the upper lip opposite the front edge of eye, which is one of the main characters in the family Echelidae. The posterior nostril is located in front of eye near the level of upper edge of eye instead of on the lip. The sixth infraorbital pore is above the level of the rictus of the jaw, the origin of the dorsal fin is above the middle of the pectoral fins, the preorbital bone is triangular in shape and the teeth are compressed in the jaws; all are characteristic of the genus *Conger* (Kanazawa, 1958, *Proc. U. S. Natl. Mus. 108(3400):221–4*). Fowler further described a row of black dots along each side of belly, fading out along front of anal fin. This is a juvenile character in *C. cinereus cinereus*. In young specimens, the row of black dots along belly is very noticeable; however, as the eels grow the black dots get fewer in number until they finally disappear. Because of the above reasons *Paramyrus kellersi* Fowler is synonymized with *Conger cinereus cinereus* Rüppell.—ROBERT H. KANAZAWA, *U. S. National Museum, Washington 25, D. C.*

THE SNAKE-EEL, *ACHIROPHICHTHYS KAMPENI*, FROM PAPUA.—In 1953, the Fourth Archbold Expedition to New Guinea brought

back to the American Museum of Natural History a rare snake-eel, *Achirophichthys kampeni* (Weber and de Beaufort) 1916. Measurements of the specimen were published by John T. Nichols, in Results of the Archbold Expeditions, Number 71, American Museum Novitates, 1955, Number 1723, but specific locality data had been lost.

Mr. Leonard Brass of the Archbold Expeditions Advisory Board has recently met the collector of this specimen, Mr. Wynn, who gave him the following locality data:

Achirophichthys kampeni (Weber and de Beaufort) 1916, 1 specimen, 505 mm. long, A.M.N.H. №20156, collected August 6, 1953 by Kenneth M. Wynn, Fourth Archbold Expedition, in a limestone cave near Maneau village, about six miles east of Biniguni village, Milne Bay District, Territory of Papua.—FRANCESCA LAMONTE, *American Museum of Natural History, New York 24, N. Y.*

SOCKEYE SALMON *ONCORHYNCHUS NERKA* WITHOUT A DORSAL FIN.—In 1954 the Pacific Salmon Investigations of the U. S. Fish and Wildlife Service began the study of the races of Pacific salmon. Sockeye (red), chum and pink salmon were collected from many areas. Research vessels from Japan, Canada and the United States took samples of fish at designated locations in the Okhotsk Sea, the Bering Sea and the North Pacific Ocean. On the North American

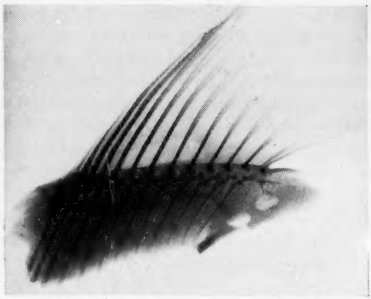

Fig. 1. Photograph of X-ray of normal dorsal fin in the sockeye salmon, *Oncorhynchus nerka*, showing dorsal fin rays, distal radial and proximal radial bones are present. (U. S. Fish and Wildlife photograph by T. O. Duncan).

continent, biolgoists collected samples of salmon from the major river systems and fisheries from the Columbia River to points north of the Arctic Circle.

In 1959, a sockeye or red salmon, *Oncorhynchus nerka*, that had no dorsal fin was collected from the Kvichak River in the Bristol Bay area of Alaska. To date this is the only example of a dorsal fin anomaly of this type noted in approximately 40,000 sockeye salmon that have been processed and X rayed at the Seattle Biological Laboratory.

A close inspection of the dorsal fin area revealed no scar, and the scale rows appeared to be

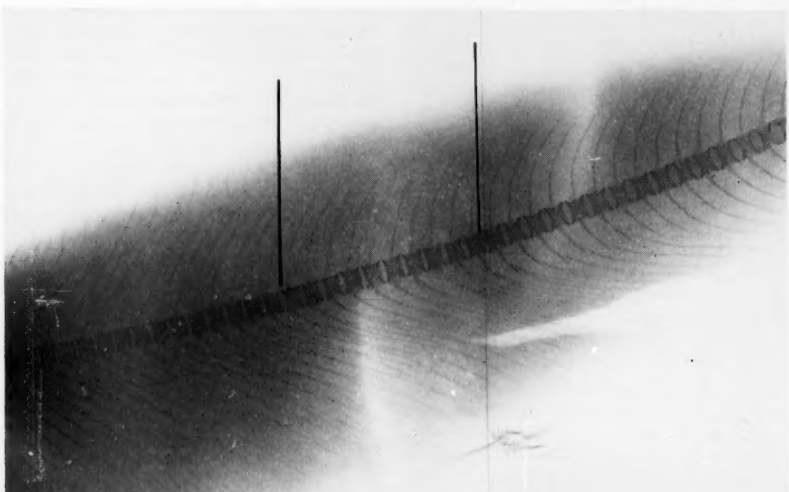

Fig. 2. Photograph of an X-ray of the abnormal sockeye salmon, *Oncorhynchus nerka*, (dorsal area blocked off) showing that no dorsal fin rays, no distal radial and no proximal radial bones are present. (U. S. Fish and Wildlife photograph by T. O. Duncan).

normal. No dorsal fin rays and no distal radial or proximal radial bones were present on the photograph of the X-ray of the abnormal fish (Figs. 1 and 2). On this basis, it was reasonably established that the fin anomaly was due to non-development of the dorsal fin. The following data were collected from the specimen: a. sex—female; b. age—5 total years (3 years in fresh water, 2 years in the ocean); c. gillraker total count—33; d. anal fin count—16; e. scale rows along lateral line—129; f. weight—1.79 kilograms (3.94 pounds, relatively small fish of the Kvichak area); and g. fork of tail to mideye measurement —498 mm.

After a review of literature, including numerous publications on tagging and marking of sockeye salmon, to the author's knowledge a dorsal fin anomaly of this type in the genus *Oncorhynchus* has not been described. Salmonids with abnormal fins are not unusual (Maxfield, 1958, *Copeia (3):232–3*; and French, 1960, *Copeia (3):247–8*). Mr. Howard Smith, Fishery Biologist of the Fisheries Research Institute (personal communication), states that he has discussed missing fins in salmon with other biologists from the Bristol Bay area, but he knows of no sockeye salmon with a missing fin. Code (1950, *Prog. Fish-cult. 12(2):85*) found a number of cutthroat trout, *Salmo clarki*, in Sheep Creek, Utah, without dorsal fins, and Jackson (1953, *Fishing Gazette [England] 135:1062*) described, and Seligman (1898, *Jour. Pathol. and Bact. 1898:1–2*) illustrated, a trout with two dorsal fins.—DONALD E. LEWIS, *Biological Laboratory, 2725 Montlake Blvd., Seattle 2, Washington.*

REVIEWS AND COMMENTS

PHYLAX TELESCOPUS-V

One of the most appalling things about so-called "Conservationists" in North America is the incontrovertable fact that of late years they have increasingly devoted themselves to destruction. Of those dealing with animal conservation, only the bird people have consistently tried to protect the creatures under their care as a whole, and they have not been entirely successful. The mammal conservationists were long ago pressured by livestock interests into active destruction of predatory mammals, to such an extent that bears, bobcats, wolves and cougars are today to be seen mostly within the rigidly protected limits of our national parks. But the so-called fish conservationists are far more blameworthy. Without any active pressure from any group, many of them seem to have embarked upon a campaign to obliterate the native fresh-water fish fauna in favor solely of "game" fishes.

That any idea of conservation of the native fauna usually stops at the water's edge is illustrated by the long-time policy of the National Park Service. Since its origin, the Service has viewed as sacrilege any interference with the native flora and fauna of the parks—even insects —but for a very long time the service not only encouraged sport fishing in the parks, but also even assisted in the introduction of non-native game fishes. While this policy has been soft-pedalled or eliminated in recent years, it illustrates the point very nicely. No group has arisen to demand protection of the native fishes, or to educate sportsmen to have some regard for our heritage of non-game fishes. And the state and federal fishery agencies have shown either complete absence of or regard for interest in the preservation of fish species save what the sportsmen's pressure groups think they want in the streams.

The matter was of relatively little importance until ichthyologists placed in the hands of fishery men the means to annihilate the fishes of almost any stream or small lake. Since the introduction of rotenone fish killers, however, the "fish conservationists," who now call themselves "fish managers," have increasingly devoted themselves to an attempt to destroy the rich native fresh-water fish fauna of North America (the "rough fish" or "trash fish"—perish the terms!) and replace it with trout, bass, and a few "forage species" such as the golden shiner.

That the ichthyologists have sat idly by and watched this destruction without saying a word is a very strong indictment of the group. So far as this columnist knows, the only appeal on record for the preservation of the native non-game fish fauna was made by himself in 1949 and was published in 1954 (*Proc. Seventh Pacific Sci. Congress, 4:691–694*). He earnestly refers readers to

that paper (although he no longer has more than a few reprints left for distribution), for in it he outlined both the problem and the need in much more detail than can be done here. However, one person cannot usually generate much interest in any crusade by himself, and the lack of interest in the subject ten years ago was profound. Even an appeal to the American Committee for International Wildlife Protection produced no effect.

Now, spurred on by the apparently total extinction of several uniqe, endemic, Arizona fish species by state conservation officers, new interest is being generated. Prof. Carl L. Hubbs and Dr. R. R. Miller are taking up the cudgels for our native fish fauna; we wish them every success and offer all the help we can give.

This columnist feels that the full weight of the A.S.I.H. should be put behind the effort. The Society should have an active permanent Committee on Fish Conservation, composed of experienced members who best know the fresh-water fish fauna of the different parts of the continent. If this Committee, like the Committee on Common Names, could be a joint committee of both the A.S.I.H. and the American Fisheries Society (each committee member a member of both Societies and appointed by both Societies), the body would be even more effective. Such a committee, if active and composed of well-known men, could wield great influence in curbing the now completely untrammeled freedom of state fish commissions to wantonly and often ignorantly destroy the native fish fauna.

Finally, the problem is not confined to North America, and such a joint committee might make its weight felt elsewhere. To this end the Committee should include one or two members who are familiar with the fresh-water fish faunas of the other continents.

* * *

In continuing this column beyond its originally projected life of one year, the columnist can say that comments so far received (by November 1960) indicate that probably more good than harm has been done by it.

One evoked comment, by Prof. Bailey (*Copeia, 1960:266–267*) on zoological nomenclature, is so impeccably documented that the unwary may feel it to be completely crushing. However, Prof. Bailey has forgotten one all-important point: Following the International Rules and International Commission in matters of nomenclature still happens to be a matter of personal preference, unless and until a police state enforces the decisions. Prof. Bailey's entire paper is based upon unquestioned and unquestioning acceptance of the Rules and Decisions of the Commission. At the time I write (November 1960) the new Rules, as totally revised in 1958 at London, are still unpublished and no ordinary zoologist knows what they are, perhaps least of all those who attended the Colloquium on Nomenclature at London, and who therefore lived through a most disillusioning experience. This columnist, a lifelong, dedicated nomenclaturist, came to a final and most distressing but complete loss of faith in the newer Gospel According to St. Francis Hemming, which not only strongly invades zoological freedom but also, by demanding referral of innumerable problems to its Court of High Priests, the Commission, defeats the primary purpose of a code of rules. It is hoped that the reasons for his loss of faith, and his perhaps temporary return to the Gospel of Old Time Prophet C. W. Stiles can be presented to a more general audience of systematists, for he feels that the principles involved are important, even if the nomenclature is not.

* * *

Dr. Arnold Grobman of the Florida State Museum, in the December Copeia, has brought forward certain points in regard to the responsibilities of museums which I believe are already familiar to most if not all museum curators, and which were, indeed, an intrinsic part of my original reference to museum responsibility in Phylax III. He seems not to have understood that I was discussing *abuse of a generally recognized right* to borrow material, and he certainly did not read carefully when he accuses me of wishing borrowers to assume part of the expenses of museum maintenance. I do think non-reciprocating borrowers should out of their own research funds reimburse museums for the time consuming work of processing the loans they demand. Some curators have written me that the problem of loans is an important and trying one, about which something should be done. Some action is in prospect. One curator estimates the cost to his museum of processing loans, in his department, to be something between $5,000 and $10,000 annually. All of them agree that loan processing is eating up more and more of the staff's own research time, and most of them comment on the poor care given the material by borrowers, or the frequent non-use of materials (or non-appearance of publications based on materials) laboriously processed and sent.

In my opinion, museums have done their fair share when they pay the high cost of maintaining permanent collections open to study by non-staff people. Those unwilling to spend their own time or research funds to visit collections should be willing to pay the extra costs occasioned by their demands for loans. Either course of action costs money, but is it the borrower or the museum who

should pay? Research funds for systematists are now common. Why should these not cover necessary borrowing? Or are museums, solely because their staffs have spent the time and money to get the collections together, and maintain them, also to be held liable to provide subsidies for the research of every person who decides he wants to borrow some of their material? This would be nothing short of penalizing energy, enterprise, and foresight for the benefit of the most casual sort of prospective researchers! If this be Dr. Grobman's idea of responsibility, I feel sure most museum curators want none of it.

* * *

Of considerable ichthyological interest is the announcement, in 1957, of a newly discovered genus and species of Percidae from Europe, a continent whose fresh-water fishes are not only relatively few but also long-studied. *Romanichthys valsanicola* Dumitrescu, Banarescu, and Stoica (Trav. Mus. Hist. Nat. "Gr. Antipa" (Bucuresti), 1: 225–244) is a swift-water fish somewhat convergent with our North American darters. Of the living European perches, it approaches *Aspro* most closely, but is said to be even closer to the Eocene *Anthracoperca*. It inhabits the Valsan River in Roumania.

Comparatively little is heard in this country of research going on in Communist China. Only a few papers have reached us, the most extensive of which is Tchung-Lin Tchang's "Report of an investigation of the fish fauna of the Yellow Sea" (1957, Chinese Scientific Institute, Marine Biological Research Unit, Shanghai; 360 pp., 206 figs., bound in boards). The work is in Chinese, but appears to be a pedestrian, systematic handbook of the shore fishes of the Yellow Sea. The bibliography indicates that not only has little except a dribble of Russian literature penetrated into China for the past 20 years, but also that Chinese systematic research on the marine fishes of North China has been practically moribund for the same period.

The late Dr. Georg Duncker (died 1953) of the Hamburg Museum long ago completed an exhaustive work on the fishes of Nordmark, that portion of northwestern Germany between the Elbe River and the Danish border. The last of the five published sections appeared in 1939 and the work was left incomplete. Duncker's manuscript has been thoroughly revised by Dr. Werner Ladiges and has now been issued complete ("Die Fische der Nordmark," Abh. Verh. Naturwiss. Ver. Hamburg, N. F., Bd. 3, Supplement, 432 pp., 1 map; Hamburg: Cram, de Gruyter u. Co., 1960). This is a very useful manual, with keys, outline drawings, natural history notes, and detailed distributional information. It includes most of the fishes of the North Sea, the Baltic Sea, and the fresh waters of northwestern Europe.

Fish paleontologists, or ichthyologists interested in the history of the West Indian marine fauna will find much of interest in Dr. Edgard Casier's "Contribution à l'étude des poissons fossiles des Antilles" (1958, Mém. Suisses de Paléontol., 74: 95 pp., 3 pls.). A large part of the fishes are from Cenozoic deposits on Barbados and Cenozoic and Cretaceous deposits on Trinidad.

* * *

American herpetologists involved in the study of geographical variation and speciation of frogs will find some useful material in the recent critical study of European *Rana* species by Dr. Hans Kauri of Lund (1959, "Die Rassenbildung bei europäischen *Rana*-Arten und die Gültigkeit der Klimaregeln," Ann. Soc. Tartuensis ad Res Naturae Investigandas Constituae, ser. nova in exsilio condita (Lund, Sweden), 2: 172 pp.). One of the principal problems he attacks is the long discussed, but of late presumably settled status of *Rana esculenta* and *R. ridibunda*. Kauri has studied these frogs in considerable detail, and comes to the conclusion that these two forms cannot be considered to be distinct species. There is a similarity to some of the problems involved in the races of *R. pipiens*, at least in a superficial way.

Dr. J. Villard of Lima continues his studies of Andean batrachians with a fifth paper, "El genero *Bufo*" (1959, Mem. Mus. Hist. Natural "Javier Prado," no. 8: 48 pp., 14 pls.). Among the species treated are *Bufo ockendeni, B. typhonius, B. marinus, B. rubropunctatus, B. cophotis*, and *B. spinulosus*.

The amphibian fauna of French Morocco is not large, comprising only ten species. These animals have now been extensively treated in a new work by G. Pasteur and J. Bons (1959, "Les batraciens du Maroc," *Trav. Inst. Sci. Chérifien* (Rabat), Ser. Zool., 17: xvi + 240 pp., 3 col. plates, 3 folding maps). This is not merely a systematic manual, but a treatise giving an excellent account of sexual dimorphism, voice, distribution, breeding habits, eggs, larvae, and longevity of the species, in addition to general chapters on amphibian classification, morphology, physiology, food, and reproduction, and on the origin of the Moroccan amphibian fauna. There is also a separate section on Arabic and Berber names as well as a good bibliography and an alphabetical index. In fact, this is one of the best regional works on amphibians that we have seen. What has hitherto been presumed to be the vicarious North African population of the large Iberian spadefoot toad, *Pelobates cultripes*, is described as a new species, *P. varaldii*.

Dr. Griffiths continues his phylogenetic studies on frogs with a paper on the relations of the strange little anurans of the Seychelles Islands (1960, Ann. Mag. Nat. Hist., (13)2: 626–640), which Noble considered to be pelobatids. Griffiths' anatomical study, on the contrary, indicates that *Sooglossus* is not a pelobatid but a ranid, and probably originated not far from the stem of *Arthroleptis*. This is of considerable zoogeographical importance, for the supposed presence of pelobatids on the Seychelles seemed almost unbelievable. No members of this family seem to be present in either India or Africa, and they are not good at crossing salt water barriers. On the other hand, the ranids are champion island-hoppers, and are common in India and Africa. This piece of research thus clarifies a good deal more than the systematic position of some very obscure frogs.

A welcome manual on the reptiles of a herpetologically poorly known area is Dr. Kamel T. Khalaf's "Reptiles of Iraq with Some Notes on the Amphibians" (1959, Baghdad, Ministry of Education: viii + 96 pp). There are illustrated keys but no figures of whole animals, and no references to the literature through the text. However, the bibliography indicates that the author used a large part of the pertinent modern literature.

Companion works to the book of Pasteur and Bons on Moroccan amphibians mentioned above have appeared in the same series. Bons treats the lizards (1959, "Les Lacertiliens du Sud-ouest Marocain," Ibid., no. 18: 130 pp., 9 pls., 4 maps) and Pasteur and Bons give a "Catalogue des Reptiles Actuels du Maroc" (1960, Ibid., no. 21: 132 pp., 5 pls.). The trio of books forms an excellent summary of the herpetology of western Barbary. G. S. Meyers, *Standford, 1 Dec., 1960.*

COMMENTS

A SHORT HISTORY OF THE DIVISION OF FISHES, UNITED STATES NATIONAL MUSEUM, DECEMBER 15, 1856 TO DECEMBER 15, 1956.—In recognition of the centennial anniversary of the division of fishes of the United States National Museum, it is fitting to review briefly its history and some accomplishments for the first hundred years.

This anniversary date was established by the first entry in the *catalogue of specimens* on December 15, 1856. It reads: "*Catostomus hudsonius*, locality Lake George, New York, collected 1850 by S. F. Baird." All that remains of that specimen today is the well preserved but dry pharyngeal bone, bearing teeth.

By searching through the reports of the Smithsonian Institution, one finds that the various departments and divisions of the Museum had a nebulous beginning.

Drs. Spencer F. Baird, Theodore N. Gill, and Charles Girard, M.D., were the first to assemble a research collection of fishes in the Smithsonian Institution. This early collection consisted of Baird's private fish specimens, along with materials collected by the U. S. Government explorations and surveys, including those of the Wilkes Exploring Expedition, 1838–1842. The oldest fish specimens, however, are some collected by Louis Agassiz in Europe during the 1820's.

Charles Girard, as a student and assistant of Louis Agassiz who showed scientific aptitude in systematic zoology, was brought to the Smithsonian Institution in 1850 by Dr. Baird. He remained until 1860 when he returned to his native Switzerland. His first big contribution based on fishes in the Smithsonian Institution was "A monograph of the cottoids" published in 1852.

Drs. Baird and Girard collaborated in this early period on several papers, which were published from 1853 to 1855.

Dr. Theodore Nicholas Gill "was included in 1859 in the group who were being paid for the preparation of zoological reports for the Northwestern Boundary Survey, and the following year he was working on the fish report for the North Pacific Exploring Expedition." Although he was not an official member of the fish division staff, most of his ichthyological work was done on the fish division collections until his death September 25, 1914.

Dr. G. Brown Goode arrived at the Smithsonian Institution in November 1872 to assist Dr. Baird. In 1873 he was given the title *zoologist*, and assisted Dr. Baird in 1873 in arranging the fish specimens at the Museum according to Dr. Gill's fish classification published in 1872. Dr. Goode was made assistant curator of the National Museum in 1875.

Dr. Baird's keen interest in the fishes of North America and his close association and study of the fish collections up to 1870 made him an outstanding authority. During a few summers spent on the coasts of New Jersey, Massachusetts, and Maine he was much impressed with factors causing a decline in abundance of food fishes along those coasts. Through the influence of Dr. Baird, Congress created the U. S. Fish Com-

mission in 1871 and Baird was appointed to serve without salary as commissioner. Immediately, Baird began to gather around him in the "department of fishes" men who could assist in the work of the new Fish Commission. One cannot distinguish where the early work of the Museum fish department was separated from the Fish Commission. Thus, the U. S. Fish Commission arose out of the fish division of the U. S. National Museum in 1871.

Dr. Tarleton H. Bean in 1877, with the title *assistant ichthyologist*, was the first official full-time staff member of the fish division. He became curator in 1880, but when his duties became too heavy with the Fish Commission he was made honorary curator from 1888 to 1905.

Barton A. Bean was made *assistant* in 1882, *aid* in 1886, and *assistant curator* in 1890, which title he held until retirement in 1932. He was in charge of the division from 1887 to 1905, when Dr. Barton Warren Evermann became *curator* from 1906 to 1913, but during that period it appears that Dr. Evermann devoted most of his time to the work of the Fish Commission instead of the fish division. B. A. Bean was in charge again from 1913 to 1932, a period in which the work of the fish division progressed very little. It represents an era of stagnation, except for the research work accomplished by visiting ichthyologists.

Dr. George S. Myers was *assistant curator in charge* from January 1933 to August 1936, and I was *assistant curator in charge* from December 31, 1936 to January 15, 1938. The fish division lacked a *curator* from 1913 to January 15, 1938, when the author received that title.

Loren P. Woods was *associate curator* from 1947 through 1948; Dr. Edward C. Raney, *associate curator* in 1949 for 3 months; Dr. Ernest A. Lachner has been *associate curator* since February 1, 1949. Dr. William Ralph Taylor was appointed *associate curator* on December 3, 1957.

Assistants or aids were: Peter Parker, 1882 to 1887; H. G. Dresel, 1882 to 1885; and R. H. Miner 1882. The next records for aids are: C. A. McKnew, 1905 to 1907; Alfred C. Weed, 1908 to 1913; expert ichthyologist, Dr. John O. Snyder, 1914; Isaac Ginsburg, aid 1917 and 1918. Earl D. Reid, aid, 1919 to 1945; Marie P. Fish, aid, 1945 and 1946; Donald Erdman, aid, 1947 to 1950; William Leapley, aid, 1948 to 1953; and Robert Kanazawa, aid, 1950 to date.

Dr. Hugh M. Smith, former U. S. Commissioner of Fishes, held the title of *associate in zoology* beginning in 1922, but worked full-time in the Museum only from 1935 to 1941. He did research work mostly on Siamese fishes.

Dr. Samuel F. Hildebrand, ichthyologist, U. S. Fish and Wildlife Service, worked full-time in the division from August 15, 1942 to March 16, 1950. Isaac Ginsburg, ichthyologist, U. S. Fish and Wildlife Service, began working full-time in the division in August 1942 and even though he retired from government service on October 31, 1956, he continued to work full-time for about two years longer.

Dr. Giles W. Mead, ichthyologist, U. S. Fish and Wildlife Service, began working in the fish division on November 1, 1956. The relationship between the U. S. Fish Commission in Baird's time and now with the U. S. Fish and Wildlife Service has been most cordial. The fish collections of that agency were transferred to the National Museum in 1942, along with Hildebrand and Ginsburg. To the U. S. Fish Commission and Fish and Wildlife Service must be given credit for a substantial percentage of the fish specimens in the National Museum.

An accurate count of the number of fish specimens in the fish division was never made and no accurate records were kept until 1933. The number of specimens in each catalogue entry was not recorded if they exceeded more than a few, instead the infinity symbol "∞" was entered. No accurate record was kept of the number of fish specimens in each accession if they exceeded about one or two dozen. For example, in the fiscal year ending June 30, 1885, 63 accessions were recorded. The number of fishes estimated received is 1,000 for that year. By checking each accession, for 13 of the 63, no count was recorded. However, by checking catalogue entries for 12 of these "uncounted accessions" one finds a total of 1,516 specimens were received, and the other accession, from the U. S. Fish Commission, *Albatross*, Gulf of Mexico Cruise, must have contained a large number because some of them are still uncatalogued and it is now impossible to determine the number of specimens received. Adding the other 62 accessions a total of 1,592 specimens was received, not 1,000 as published in the report for 1885. The same errors appear to have been made during the first 75 years of fish division history.

The manuscript report for 1889 states that 115,000 fish specimens were received, but the published report lists 6,000 with the total number in the division as 107,350. Thus, in one year more fish specimens were received than the estimated total number in the division. The published report and typewritten reports from 1909 to 1914 list 500,000 fish specimens without change, yet during that period the same records indicate 76,000 specimens were received.

Dr. Tarleton H. Bean in his report for the fiscal year ending June 30, 1887, made the first rough estimate of the extent of the collections in the fish division. He estimated the number of fish specimens as follows: Exhibition 34,000; Reserve 41,000; Duplicates 25,000; Total—100,000.

By actual count in February 1887 there were 24,069 jars; 208 tanks, 4 barrels, 64 stuffed fishes; 1,086 casts; 1,354 drawings; 281 wood cuts; and 913 types of new species in the fish division. Catalogue entry 39,118 was made in June 1887. Dr. Bean states: "to this number should be added a great many extra-limital species, principally described by Dr. Gill, and a large number of types of West Indian fishes described and contributed by Prof. Felipe Poey."

"In 1887 the National Museum had more specimens in the collection of fishes than the British Museum, but they represented a smaller number of species. The British Museum at that time had 5,177 species represented by 29,275 specimens." "... The number of specimens in the collection must not be less than 100,000, which is probably the greatest number possessed by any museum in the world."

Because of these and other inconsistencies, Dr. George S. Myers, assistant curator of fishes, in his published report for 1936 re-estimated the number of fish specimens and raised the number by about 348,000, making a total of 1,103,106 fishes. That number was a conservative estimate. It did not take into consideration the large collection of larval and juvenile specimens which must number over a million specimens, all unsorted, as yet uncounted, and uncatalogued.

At the end of the fiscal year (June 30, 1957) there were 1,590,678 fishes in the National Collections.

For successful research the fish specimens in the big storage room must be arranged phylogenetically so that any catalogued species can be found on the shelf within 2 or 3 minutes. At the present time among over 170,000 jars, any lot bearing a scientific name can be located that quickly.

We read in the typewritten report of the fish division for June 30, 1893, "A general rearrangement of the collection is badly needed. That in use is according to Dr. Gill's arrangement of the Families of Fishes, published by the Smithsonian Institution in 1872, and is quite unsuited for the present time."

The fish specimens were moved to the "New National Museum" building during July and August 1910. In the report for the fiscal year ending June 30, 1911, the following statement was made: "The collections have been tentatively arranged in accordance with Doctor Gill's arrangement of the families of fishes somewhat modified by the Doctor and are, for most part, placed on the stacks in their proper family arrangement, 324 families of fishes being recognized."

Our present arrangement of fish "families" is much the same because it is too costly for major rearrangement. However, many changes have been made to bring the fish groups in better phylogenetic sequence.

There have been 157,424 entries in the catalogues during the past hundred years. These entries are shown in 10 year periods, from December 15, 1856 to December 14, 1956.

December 15 to December 14	Number of catalogue entries
1856–1866	5,589
1866–1876	10,661
1876–1886	12,079
1886–1896	9,652
1896–1906	9,141
1906–1916	20,732
1916–1926	10,414
1926–1936	10,593
1936–1946	36,313
1946–1956	32,250

A tabulation was made of various items in the division of fishes on December 15, 1956. There are 25 steel filing case drawers filled with drawings and photographs of fishes totaling by conservative estimate 9,200 items, filed alphabetically by genus and species. The 2 steel filing case drawers containing photographs of ichthyologists started in 1937 now totals 476 individuals. The division library includes most of the important books on systematic ichthyology, and in 1937 an author-alphabetized reprint library was started which now occupies 16 four-drawer steel filing cases and by conservative estimate contains over 14,000 separate items.

By actual count there are in the fish division the following number of containers and steel shelves used in preserving fish specimens:

Tanks (190 gallons capacity)	5
Tanks (64 " ")	20
Crocks (12 " ")	496
Quarter unit cases containing fish skeletons	50
Steel shelves (each 3 sq. ft. area)	2,944
Steel shelves (each 4 sq. ft. area)	635
Steel shelves (each 3 sq. ft. area) holding empty jars, laboratory supplies, or specimens under study by staff in their laboratories.	747
Total	4,897

If all the steel shelves in use in the division of fishes were laid end to end they would extend 13,613 feet, or 2⅗ miles.

By actual count there are 7,546 type lots; 4,103

of these are holotype lots and 3,443 are paratype lots. Waiting for publication are 137 holotype lots and 306 paratype lots.

By sample counting it was found that each square foot of steel shelf space in the alcoholic storage averaged 15 glass jars. Multiplying that figure by the number of square feet of steel shelving used for specimen storage we have by estimate 170,580 glass jars in use in the division of fishes.

A survey of the number of research publications by staff members during the past hundred years has been difficult to determine because accurate records were not kept until 1934. The data in the following table were compiled mostly from the published reports of the Smithsonian Institution and hand-written reports still on file in the Museum. Previous to 1887–88 records are too incomplete to be included.

Ten year period	Number of published papers		Number of figures, plates and pages published by division staff		
	Outside authors	Division staff	figs.	plates	pages
1947–1957	225	76	980	134	2760
1937–1947	139	89	326	124	2180
1927–1937	69	16	76	2	321
1917–1927	44	8	8	4	152
1907–1917	102	21	24	24	151
1897–1907	149	21	26	14	152
1887–1897	188	214	11	202	1133

LEONARD P. SCHULTZ, *U. S. National Museum, Washington, D. C.*

REVIEWS

FAUNA REPUBLICII POPULARE ROMÎNE: Vol. XIV, Facicicula 1, Amphibia. by Ion E. Fuhn. 288 pgs., 207 figs. Editura Academiei Republicii Populare Romîne, Bucarest, Rom., 1960.—This volume treats of what is known of the Amphibia of Romania (21 spp. or subspp.), and also mentions others from adjacent countries which may be collected later within its area. After a short historical survey of amphibian studies dating from Rösel von Rosenhof (1758), a general section presents a concise summary of external and internal morphology, reproductive habits, protective mechanisms, paleontology, phylogeny, and ecological relationships. Included are world distribution maps of most of the recognized amphibian families. A bibilography of 4 pages ends this section.

Most of the remainder, beginning on page 107, is the "Partea Sistematică" in which each Romanian form is treated in detail. Synonymies, descriptions, measurements, notes on habits and ecology and spot distribution maps for the country are given. For most forms the European or Eurasian distribution is also mapped. Keys are presented, including one for larval forms of Salientia.

The work is printed in Romanian and is evidently intended to serve both scientists and the general population. The choice of information to be included is excellent for this double purpose and the figures and maps are large, clear, and excellently executed. Because of the language barrier, I am not competent to judge its style; but its organization is excellent and its basic information accurate. A few errors occurred in printing, most (but not all) of which are listed in an *erata* at the end of the volume. The only one of consequence noted is the reversal of legends for figs. 200 and 206, the first being of the cranium of *Rana arvalis wolterstoffi* but labeled *R. a. arvalis*, the second of *R. a. arvalis* but labeled *R. a. wolterstoffi*.

A rather unusual circumstance occurs. Nowhere do I find an author mentioned. The only hint is the initials, "I. F.", signed at the end of a very short introduction. For this reason, I wish to state that I know the author to be as stated above. I have corresponded with Mr. Fuhn for several years, including discussions of this work which he had in preparation.

My overall appraisal of this work is that it is an excellent survey which will well serve its intended purpose for the Romanian people. For American students it is an excellent reference on amphibians in central Europe, especially for students well versed in the Romance languages, even though not knowing Romanian.—ARTHUR N. BRAGG, *Department of Zoology, University of Oklahoma.*

NATURAL HISTORY OF THE ORNATE BOX TURTLE, *TERRAPENE ORNATA ORNATA* AGASSIZ. By John H. Legler. Univ. Kansas Publ., Mus. Nat. Hist., 1960, Vol. 11, No. 10, pp. 527–669, 16 pls., 29 figs. $0.25 mailing charge on request to museum.—For more than a

decade the vertebrate fauna of the grassland-forest transition of eastern Kansas has been the subject of studies by Henry S. Fitch and his associates. The resulting herpetological life history monographs and general ecological papers have been of commendably high standards, but for some unknown reason, perhaps bias in favor of hard-cover tomes, none of these papers has hitherto received notice in *Copeia*.

The present volume by John Legler is a summary of four years work upon the ornate box turtle. An intensive study was carried out on some 200 marked turtles on a 220 acre area of mixed forest, prairie, and farmland. Supplementary data were gathered from specimens collected or observed in nearby parts of Kansas. The accumulated data have been condensed in a very satisfactory manner under forty topical headings. There are notable sections on the ovarian and spermatogenic cycles, growth, temperature relationships, population structure, and activity cycles. Comparisons and discussions are interwoven with the original material in an effective presentation.

Naturally the wealth of new information poses questions for a miscellany of further investigations. Among the desiderata I would place precise descriptions of mating behavior in *Terrapene ornata* and *carolina*, including information on sex recognition (musk glands are present but their function is unknown; visual detection ability is apparently quite good). Data on the sex ratio in juveniles might clarify the unbalanced ratio in adults reported by Legler (possibly a differential mortality rate is unfavorable to males). Further study of the characteristics of females that lay two clutches of eggs in a season also seems called for. And, as Legler points out, the meager data on homing behavior leave much to be explored. Such queries for the future indicate the range of material and problems that Legler has touched upon.

In sum, the volume covers in a generally successful fashion the author's stated objectives of amassing information on the life history and adaptations of *T. ornata*, comparison of the data with those on other turtles, and determination of geographically limiting factors and the synecological role of these turtles.

This sort of study on a relatively common animal would be eminently suitable for rewriting in a popular version. Expositions along the lines of the German Neue Brehm-Bücherei and the English New Naturalist Monographs could do much to educate and interest non-professionals in our field and might be profitable for ordinarily impecunious naturalists.—GEORGE B. RABB, *Chicago Zoological Park, Brookfield, Illinois.*

EDITORIAL NOTES AND NEWS

News Notes

THE new building of the Narragansett Marine Laboratory of the University of Rhode Island was dedicated on October 8, 1960. The previous building was destroyed by fire. DR. CHARLES J. FISH is the director.

DR. DON HUNSAKER II has joined the staff of the Department of Zoology, San Diego State College. Dr. Hunsaker is continuing his studies of Sceloporine Lizards.

DR. BRUCE B. COLLETTE has completed his doctorate at Cornell University and has joined the staff of the Ichthyological Laboratory of the U.S. Fish and Wildlife Service. Dr. Collette is completing his studies on the percid sub-genera Hololepis and Villora, and is also working on western North Atlantic Hemiramphidae and certain problems in tuna systematics.

Three translations of Russian fish papers are available for distribution. Requests should be addressed to: Ichthyological Laboratory, U. S. Fish and Wildlife Service, U. S. National Museum, Washington 25, D. C. The papers are:

MAKUSHOK, V. M. The Morphology and Classification of The Northern Blennioid Fishes (Stichaeoidae, Blennioidei, Pisces). *Trudy Zool. Inst. Akad. Nauk SSSR, 1958, vol. 25, pp. 3–129.*

SVETOVIDOV, A. N. Materials on the Structure of the Fish Brain. 1. Structure of the Brain of Codfishes. *Trudy Zool. Inst. Akad. Nauk SSSR, 1953, vol. 13, pp. 390–419.*

SVETOVIDOV, A. N. Note on *Phycis borealis* Saemundsson (Pisces, Gadidae). *Trudy Zool. Inst. Akad. Nauk SSSR, 1955, vol. 17, pp. 346–348.*

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